CONTRIBUTION TO THE COMPARATIVE ANATOMY OF THE EARED AND EARLESS SEALS (GENERA ZALOPHUS AND PHOCA)

By A. Brazier Howell,
Collaborator, United States National Museum

FOREWORD

The interest of anatomists has long been intrigued by the Pinnipedia and it is probable that no order of a comparable size has been more often investigated from this standpoint. The pinnipeds have a very important place in the program of the author relative to his investigation of aquatic adaptations in mammals and he at first thought that this work with the order would be rendered relatively easy by the apparently full reports upon both the myology and osteology, illustrated in some cases by handsome plates, with which he was casually acquainted. Only a little investigation was needed, however, to establish the fact that these reports were not of great aid, for they are chiefly descriptive, and many discrepancies were apparent.

Of the earlier dissections of pinnipeds those by Duvernoy (1822), Humphrey (1868), and Lucae (1873) are all important, although some of their details are to be viewed with suspicion and many of their conclusions are extremely unlikely. But scant attention need be paid them in the present report, however, for their details are well incorporated in the paper of W. C. S. Miller (1887), who discusses them with really unnecessary fullness, and their inclusion here would not only constitute repetition, but would be otherwise undesirable as befogging the report to a bewildering degree. Comparisons have therefore been made only with the findings of Miller and Murie, where these investigators differ from conditions as encountered by me. Miller was an accomplished anatomist who dissected a variety of pinnipeds, presumably with great skill. His text treats fully of a *Phoca vitulina* and an *Arctocephalus*, although comparisons are made where desirable with several other phocids and an *Otaria* (=*Eumetopias*). A serious defect, however, is that his report is unillustrated as far as concerns the musculature, and his de-

scriptions are often so involved and bristling with details, unimportant save when a study is being made of individual variation, that one is often at a loss to fathom his exact meaning. He made some mistakes in interpreting what he saw, and doubtless others which it is difficult to discover, but one gathers the impression from working with his paper that he was a capable, trustworthy man, doing work of a high order of merit.

Murie's reports upon the myology of *Eumetopias* (his *Otaria*) (1872) and *Odebenus* (his *Trichechus*) (1870) are descriptive rather than comparative. They are accompanied by beautiful plates some of which are far more satisfactory than any I could execute, but others are vague and misleading. He misnames and misinterprets a number of muscles, although to but a slightly greater extent than did Miller. It is, of course, beyond question that Murie was an able and brilliant human anatomist, but it is perhaps not out of place for me to say that after working with his sea lion and *Globiocephala* reports line by line I have received a definite impression that implicit reliance can not always be placed upon the myological details which he presents.

One might, therefore, justifiably enquire regarding the value of an additional report upon the anatomy of the Pinnipedia. The reason is that the others are largely descriptive or compare individual muscles, but no one has heretofore analyzed the differences occuring in the otariids and phocids, the significance of these from a functional aspect, the reasons for the osteological peculiarities, and the organization of the pinniped as a dynamic machine built for aquatic locomotion. My myological report is but a necessary part of the whole. The conclusions to which the anatomical evidence points has not been discussed in entirety, however. Most of the myological discussion is presented with the muscles, some of the osteological with the bones, and still more under the general discussion. Yet additional facts and theories are being reserved which are considered to belong more properly with a comparison of the Pinnipedia with other aquatic mammals. I have placed those interpretations upon the anatomical peculiarities of the Pinnipedia which to me seem most logical, but it can not be claimed that all of these are correct, or that some of them will not need modification when additional facts are brought to light.

In the drawings of muscles no especial system of reduction is used, the proportions being merely such as will fit conveniently upon a page. In the bone drawings, however, comparative details are presented to represent relative difference in size, and because the trunk length of the *Phoca* skeleton used in comparisons was seven-tenths that of the *Zalophus*, the reduction of the latter's bones is but seven-tenths of those of the former. In this way one may more readily compare osteological details.

HABITS

For a proper understanding of the pages that follow it will be necessary briefly to discuss the habits of the eared and earless seals, and to mention certain acts which their form allows them to perform or prevents them from doing.

Zalophus californianus, as representing the sea lions or eared seals, is fundamentally a long, rather slender animal, save when very fat or in the case of mature bulls, which spend considerable time on land but seldom venture farther than a few yards away from the sea. The fore and hind limbs are both highly modified into paddles and considering the highly specialized condition in this respect, terrestrial locomotion is accomplished with more agility than one would imagine

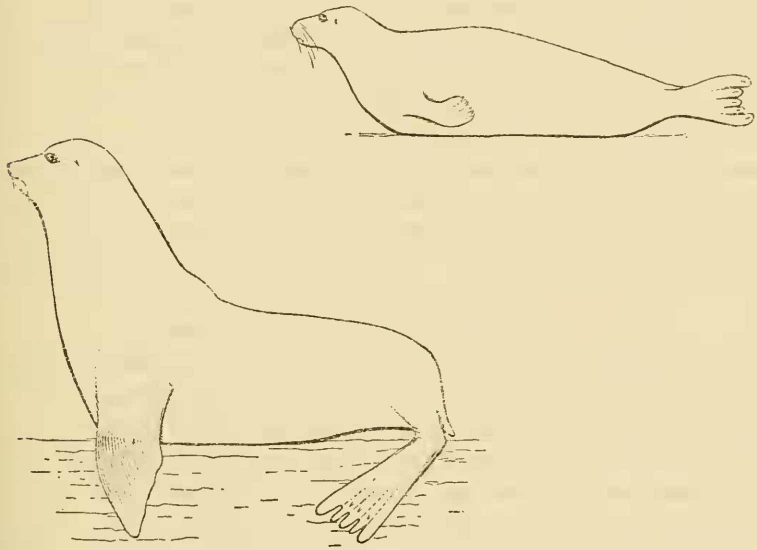

FIG. 1.—TYPICAL TERRESTRIAL POSTURES OF AN EARED SEAL (SEA LION OR OTARIID, ZALOPHUS) AND EARLESS SEAL (TRUE SEAL OR PHOCID, PHOCA, ABOVE)

to be possible, and the animal travels on land much as would a fissiped carnivore with legs of equal length, galloping about with considerable speed. The neck is extraordinarily mobile, enabling a trained sea lion to perform surprising feats of balancing with its nose, probably to a more perfect degree than could any terrestrial mammal. Marked flexibility of the lumbar region also exists, and otariids—especially fur seals—can contort this part of the back in a striking manner. The forelimb is used as the primary and almost exclusive means of aquatic locomotion, and as the chief support for the body when on land. In the latter situation the manus is bent at the wrist and extended laterad. The pes is also bent at a right angle to the shank, but as the shin is bound down to the pelvis, so as

to be held within the body contour and virtually immovable, the only way that the foot can assume the plantigrade position used in walking is for the sacral vertebrae to be forced into a position that is practically vertical to the ground, which is done with ease. The hind limbs apparently play a much less important part in swimming than one would infer from the degree of specialization which they exhibit.

The *Phoca hispida*, as typifying the earless seals or phocids, is really a very different animal. It, too, is stream line in form but in a somewhat different manner from the otariid. Usually fat, it is of greater circumference than the otariid of the same mass, excepting adult bulls of the latter, and in most forms at least is relatively shorter. The shortness of the neck seems especially marked and to a greater degree than is actually the case, for it is very wide, tapering to the broad thorax. The neck is not markedly flexible, as is that of the otariid—in fact, it is probably less so than in the average fissiped, and one gains the impression that the entire trunk is less agile than in the sea lion. The forelimbs are weak, are not used as a primary means of propulsion through the water but in lateral, water-treading movements, and their use on land is limited to such acts as aiding in the surmounting of a low obstruction. Swimming is accomplished by a rhythmic, transverse movement of the hind feet, presented palm to palm, the movements being on the whole comparable to those of a fish in swimming. Both otariids and phocids may swim for considerable distances on the back, but the former assumes this position evidently for brief periods only, while the latter is more prone to do so, at least in captivity. For several anatomical reasons, as discussed later, the Phocidae can not place the hind foot to the ground in a plantigrade manner and apparently never attempt to do anything with the feet while on land save keep them, palm to palm, elevated well out of harm's way. Terrestrial progression is accomplished by a caterpillarlike wriggling in the sagittal plane—not in the horizontal or transverse one—with the forefeet close to the sides and the hind ones elevated above the ground.

MATERIAL

The material assembled for the present work was not all that was desired but was the best that could be procured. As representing the Phocidae an embalmed subadult female of *Phoca hispida* taken by H. C. Raven, Ponds Inlet, Baffin Island, August 30, 1926, was obtained by exchange from the American Museum of Natural History. But a single skeleton, partially articulated, of this species could be located and that was borrowed from the Museum of Comparative Zoölogy through the courtesy of G. M. Allen. It is of a

subadult, unsexed, and bears the number 6297, from Cumberland Gulf, April, 1878, collected by L. Kumlien. As representing the Otariidae, the National Museum secured through the interest of the Johns Hopkins Medical School an embalmed juvenal female *Zalophus californianus* that died September 6, 1925, after being at the Baltimore Zoological Park for only a short time. Sundry anatomical observations were also made upon a large adult female of this species that died at the National Zoological Park during June, 1927. For osteological comparison the most suitable skeleton available was that of a subadult male, disarticulated, No. 200847 of the National collection, that died at the National Zoological Park December 19, 1915. There was also at hand some less satisfactory skeletal material of this same species, some of *Phoca*, mounted skeletons of both families, and an extensive collection of skulls. It should be understood that in the following pages the above specimens, upon which the present study is primarily based, are referred to not by number, but by such terms of designation as " the otariid " (the embalmed specimen for the muscles, and the skeleton for osteological details), or " my phocid." My study of the prepared specimens has been supplemented by observation, as often as possible, of both wild and captive specimens of *Zalophus* and *Phoca* (of the *vitulina* and *richardii* sorts).

EXTERNAL FEATURES

The length from nose to tip of tail was 978 in the *Zalophus* and 1,019 mm. in the *Phoca*, so these embalmed specimens were as nearly comparable in size as one could reasonably wish. The length of tail in the former was 60, and in the latter 72 mm., and the circumference of the thorax respectively 430 and 780 mm. The sea lion was excessively emaciated and not only was there no fat but most of the muscles where somewhat shrunken. The seal, on the contrary, was very fat, this being tender and free from fibrous tissue. Over the shoulder it was about 30 mm. in thickness, thinning toward the head, caudad in the region of the hind flippers, and upon the forelimbs. In a state of nature females and immature males of *Zalophus* are usually sleek and of slender appearance, although captive specimens and old males may become fat and logy; but it is normal for at least most of the Phocidae to have an extensive blubber layer. All pinnipeds have a form that is markedly " stream-line " but which animal is the more efficient in this respect we do not know. Both are covered with short stiff hairs, the pelage of the phocid being the thicker.

In the otariid the mystacial pad had a width of 40 mm. and appeared rather narrow. The vibrissae were directed chiefly caudad

and the nostrils were directed at an angle of about 15° or possibly 20° rostro-dorsad of the cranial axis. The mystacial pad of the *Phoca* had a width of 75 mm. and appeared very wide and as though inflated. The vibrissae were directed mostly laterad, but also downward and forward, and the whole mystacial area was more walrus-like than that of the otariid. The nostrils were directed rostro-dorsad at an angle of about 45° to the cranial axis, thus being situated more dorsad than in the sea lion. The direction of the eyes in the otariid was at an angle of about 50° with the vertical, and about 15° in the phocid. The eye was larger in the former, the width between the canthi being 70 mm., and in the phocid 40 mm. The latter had a few supraorbital vibrissae, which were entirely lacking in the former. In the *Zalophus* the pinna of the ear is slender and with a length of 28 mm., while the *Phoca* has no pinna. In both animals the auditory tube is of considerable length, but because of the more arched cranium of the otariid, especially in old males, the audital orifice is located relatively less dorsad than in the phocid. Thus, in the latter the nostrils, eyes, and ears occupy a position more decidedly dorsad.

The neck of a small otariid is very mobile, and as it is relatively slender, it appears longer than the very broad neck of a phocid, tapering, as it does, to the head. In the eared seals the necks of bulls develop to an astonishing extent, however, this being partly muscular for combat and partly fatty. In this family the base of the neck and thorax are cylindrical, or even slightly flattened transversely in form, while in *Phoca* the tendency has been farther away from the typical terrestrial carnivore and there is an appearance of slight flattening dorso-ventrad. The whole body appears definitely longer in the sea lion, but this is difficult of proof. In this animal the lumbar region is exceedingly limber, because of the elasticity of the intervertebral disks and the form of the vertebrae themselves, this being so largely as an aid to terrestrial locomotion; but such is not the case in the earless seals, in which there is apparently no marked ability to bend the lumbar region ventrad. In the otariid the tail was virtually conical with a length of 60 mm., but in the phocid this member, 72 mm. long, was flattened dorso-ventrad, measuring 43 mm. in width by 25 mm., and fit nicely into the angle formed by the adpressed hind flippers.

In the otariid the axilla[1] was at a point a trifle proximad of the center of the ulna, but in the *Phoca* it was opposite the ulnare. In the former the visible portion of the fore leg had a length of 300 mm. from the axilla and was very highly modified as a paddle, being

[1] The term axilla as herein used is employed to designate the ventral and caudal juncture of the fore limb with the body, not in its more precise meaning of the region beneath the shoulder joint.

thicker and longer upon the cranial border and thinner and shorter upon the caudal one. Each digit had a minute circular nail set within a pit in the integument, located approximately at the end of the terminal phalanx, and a cartilagenous prolongation of the digits extending considerably farther. The distance from the metatarso-phalangeal joint of the first digit to the nail was 85 mm., and from the nail to the termination of the digit, 65 mm. The entire manus was rather stiff, without free movement of the digits, and there was a minimum of possible abduction or adduction. The interdigital membrane reached to the ends of the digits, and the sole was naked and wrinkled. In the *Phoca* the external part of the foreleg measured but 100 mm. from the axilla and was not highly modified into a paddle. The manus was short and broad and hairy upon the palm, it was abducted more than in most mammals, and the articulations of the carpal bones were loose to the touch. As in the otariid the first digit was the longest, and there was sequential diminution to the fifth, but in that animal the difference in length between these two was very marked and in the phocid very slight. There are broad, heavy nails upon all the digits of the latter, and there are no cartilagenous extensions.

The crotch, between the hind limb and tail, was in the otariid at the most caudal of the muscles between the innominate and the leg, but in the *Phoca* conditions differed, for there was a considerable distance between the crotch and the last muscles, this being occupied by tough fatty tissue. In the former animal the crotch was opposite the middle of the calcaneal tip (heel), while in the phocid it was located about 20 mm. farther caudad, a distance not sufficient to make much difference in the mobility of these members. As discussed more fully elsewhere the hind foot of the otariid readily assumes a plantigrade position at an angle of 90° with the shank, while in the *Phoca* the angle so formed, without undue forcing, does not exceed 60°. From the crotch the hind limb of the latter measured 220 mm. in length, and of the otariid, 260. When viewed from the rear with joints as relaxed as it was possible to get them in the preserved specimens the plantar planes of the feet of the otariid presented the appearance of a very steep-sided V, and in the *Phoca*, of an equally steep-sided Λ. Pronation and supination corresponded with these positions, but so little of the leg projected from the body that one could not determine the precise amounts. In both animals the first and fifth digits are considerably the most robust and the longest. In the *Zalophus* only there is also a cartilagenous extension to each digit. The distance from the metatarso-phalangeal joint to the nail of the first digit measured 77, and from the nail to the tip of the toe, 78 mm. The cartilages of the middle three digits were relatively a bit shorter, and that of each toe projected beyond the interdigital membrane, as shown

in Figure 24. The extended breadth of the hind foot at the nails was 133 mm., but the difference between the collapsed and extended width was slight. Upon the first and fifth digits there were little more than nail pits, as in the case of the fore foot, but the nails of the middle digits were long, slender, and almost straight. Unlike the case of the fore foot, the digits of the pes in this genus are capable of considerable flexure, even to the cartilages, and the latter may be flexed out of the way of the nails, permitting the use of these in scratching. The sole is naked, but is covered with hair in the phocid. In the latter the first and fifth toes are relatively more robust than in the otariid and possible abduction of these digits is much greater, partly because of the more generous width of the interdigital membrane. Thus the greatest width of the foot at the base of the nails was 190 mm. in this specimen. Whereas in the otariid the static posture assumed by the hind feet in the water is usually somewhat trailing and relaxed, in the phocid they are usually adpressed and, especially on land, carried straight out behind and unsupported. All five digits have exceedingly slender, almost straight nails.

OSTEOLOGY.

It is intended here to present not a complete description of the skeleton of two species of pinnipeds as such, but rather to compare critically two skeletons which are considered to be representative of the families Otariidae and Phocidae. Minor differences in the interrelationship of the bones of the skull are not dwelt upon, but rather is it intended to enumerate and attempt to evaluate those differences which are belived to be functional, as well as the phylogenetic ones, to discover why and to what degree pinnipeds differ from fissipeds, and in just what manner otariids differ from phocids. The osteology of the pinnipeds has been described by a number of others but no one heretofore has investigated the mechanical and myological reasons for their osetological details.

It has been impossible in the present instance to accumulate skeletons of all, or even satisfactory material representing the majority of, pinnipeds, but comparisons of skulls have been made, family characters as based upon cranial details have been checked over, and where the characters of the otariid or phocid differ from those common to their respective families, these are mentioned.

Other than of juveniles but one skeleton of *Phoca hispida* (No. 6297, Mus. Comp. Zoöl., Cumberland Gulf, April, 1878, sex unrecorded, by L. Kumlein) could be located, and this is compared with one of a subadult male *Zalopus californianus* (No. 200847, U.S.N.M., from National Zoological Park, December 19, 1915) which is nearer the same age than any other at hand. For comparison certain meas-

urements and percentages are also presented of the skeleton of an adult cat (*Felis catus*).

Some vertebral measurement was needed as a standard of comparison but it was thought advisable to exclude from this the cervical series. The sum of the length of the thoracic, lumbar and sacral vertebrae has therefore been taken as a yardstick. It was found that this measurement in the *Phoca* skeleton was almost precisely seven-tenths that of the *Zalophus*. In drawings of single bones of the latter the scale is, therefore, as though the osteological details of this individual were precisely seven-tenths of their true size. Attention should be called to the fact that classification of the osteological characters as being of myological or phylogenetic derivation is at times arbitrary and purely for convenience. Any character doubtless become phylogenetic if present for a sufficient length of time. By "transverse process" is meant any vertebral process situated laterad without reference to its homology, as of the atlas or of a sacral vertebra.

SKULL

The illustrations give a better idea of the general form of the skull than can a description. That of the *Zalophus* is long and narrow, and in the *Phoca* short and broad, most of the difference in length occurring anteriorly. In the *Zalophus* the skull is 27 and in the *Phoca* 23 per cent of the body length. In the same order the glenoid-rostral measurement is respectively 70 and 61 per cent of the total length of the skull, and that for breadth to length is 53 and 66 per cent respectively. Beginning rostrad it is seen that there has been a slightly greater recession caudad of the anterior nares, relative to total length of skull, in the *Phoca*. In the *Zalophus* there is a well defined process formed by the premaxillary tips, which is absent in the *Phoca*. The reason for this is apparently either muscular or possibly cartilagenous, but nothing to account for it was met during dissection. Similarly the anteorbital processes of the maxillae, present in *Zalophus* only, should be due chiefly to details of the orbicularis oculi, and possibly also the frontalis, but as mentioned later I am not reporting upon the facial musculature. The absence of supraorbital processes in the *Phoca* and their presence in *Zalophus* is correlated first with the lack in the former of a distinct "interorbital" extension of the temporalis, with the greater size in that animal of the eyes and the true orbits (as distinguished from the anterior temporal fossae), and their more dorsal position, or rather, the more pronounced ability of the eye to look straight up. This more dorsal direction of sight can be accomplished in two ways—(*a*) by a bowing out and broadening of the zygomatic arches, accompanying which change there must be either a decided increase in the strength of the

masseter muscles or a corresponding increase in the breadth of the lower jaw, accompanied by certain rather complicated changes, both muscular and osseous, in the region of the palate; or (*b*) by a decrease in width of the interorbital septum, to this extent allowing the eyes to roll upward and inward. The interrorbital septum of all pinni-

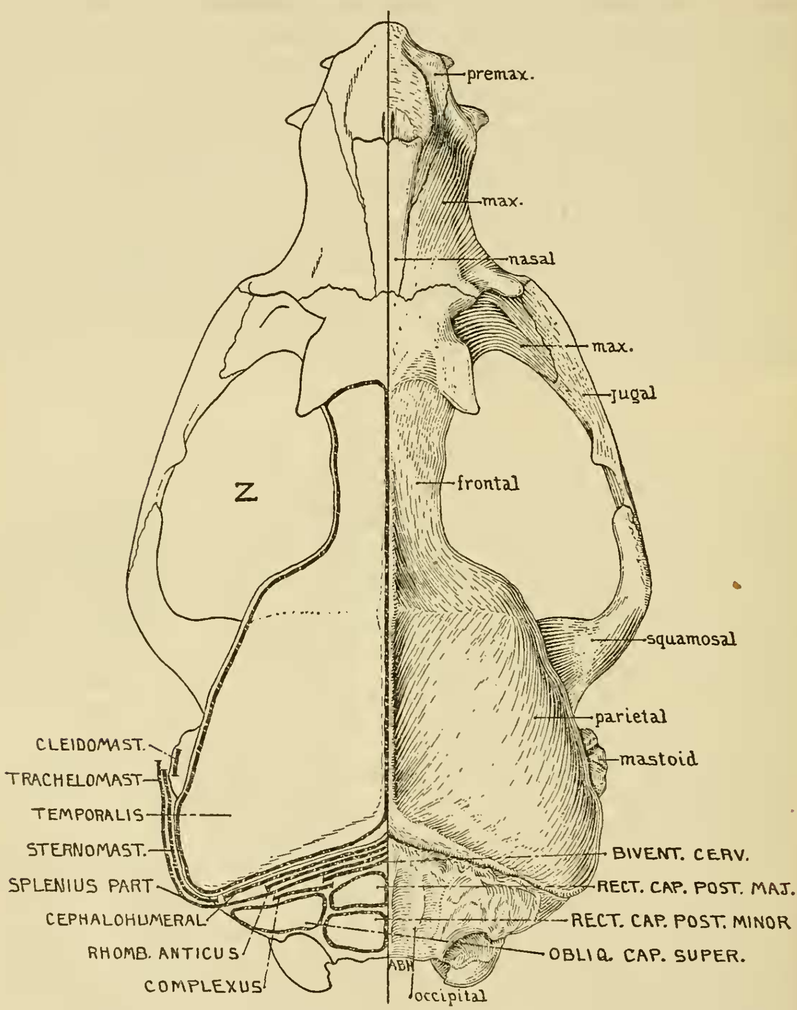

FIG. 2.—DORSAL VIEW OF THE SKULL OF ZALOPHUS SHOWING AREAS OF MUSCLE ATTACHMENTS LABELED IN CAPITAL LETTERS; NAMES OF BONES IN SMALL TYPE

peds is proportionately thinner than in existing terrestrial carnivores, indicating that even in the *Zalophus* in which interorbital breadth is 11 per cent of total skull length, dorsal vision is used considerably. In the *Phoca*, however, this is excessively thin, its width dorsad being but 3 per cent of the length of the skull, and more

ventrad almost paper thin, allowing the animal to look straight up with ease. In some of the Phocidae (as *Stenorhynchus*) the interorbital septum is not more reduced than in the sea lion, the skull is long and narrow and the orbit is not especially large. In the *Phoca hispida*, as previously mentioned, the zygomatic width is relatively great and the orbit proper, large. The size of the eye has resulted

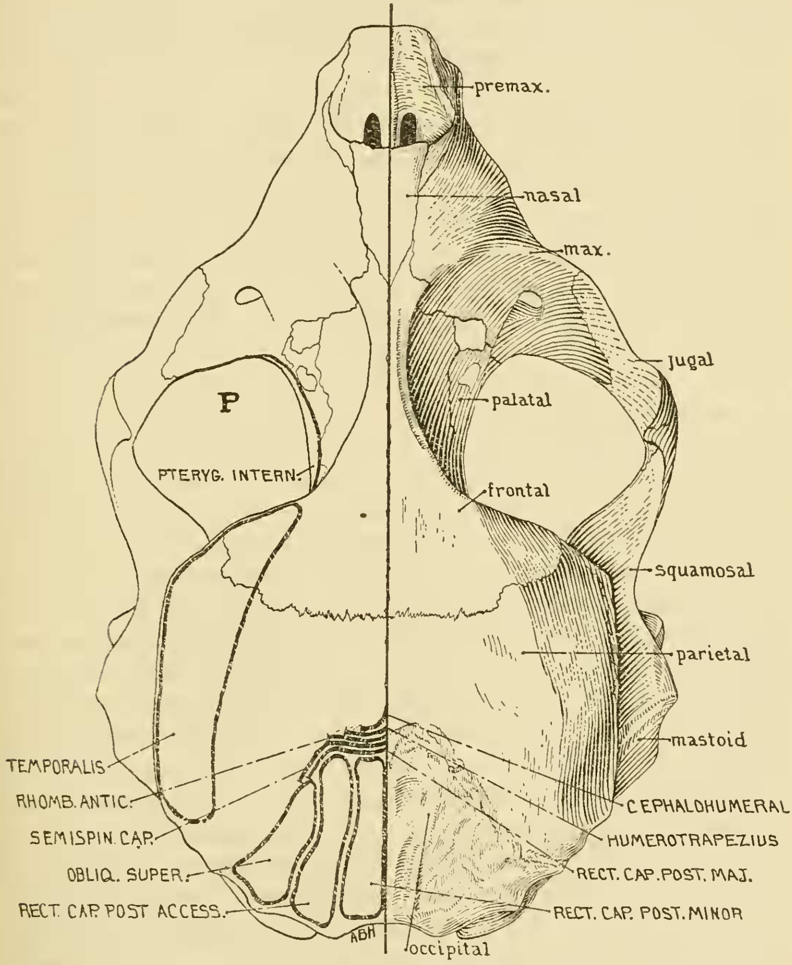

FIG. 3.—DORSAL VIEW OF THE SKULL OF PHOCA HISPIDA, SHOWING AREAS OF MUSCLE ATTACHMENTS AND (IN SMALL TYPE) NAMES OF BONES

in the forcing caudad of the postorbital process of the zygoma to a point immediately caudad of the malar-squamosal suture, while in *Zalophus* (and some phocids, as *Stenorhynchus*) this process is located considerably craniad of this suture.

Within the orbit it is seen that the excessive thinness of the interorbital septum of *Phoca hispida* has crowded the ethmoturbinals to

such a degree that these have actually forced their way here and there through the fragile frontals which overlie them. An occasional *Zalophus* skull has what appears to be an imperforate lachrymal between the maxilla and frontal just within the orbit. In the search for this bone in the Phocidae one needs be careful to identify the maxilloturbinal, a smooth part of which is often to be seen on the border of the orbital vacuity. Certainly the bone is entirely absent in the vast majority of phocids, having either dwindled and disappeared from the maxillo-frontal suture, or what seems more logical, has been forced by the enlargement of the orbit relatively farther caudad, and now represented perhaps by cartilage within the confines of the maxillo-frontal vacuity, which cartilage would disappear during cleaning of the skull. In *Stenorhynchus* only among phocids have I been able to find a bone which might represent the lachrymal and the homology of this is uncertain. In a single skull of this genus there is a small bone bounded by the vacuity, maxilla and palatal which may be the lachrymal. The maxillo-frontal vacuities of the orbit are usually much larger in the otariids than phocids, although the smallest in the former may be no larger than the greatest in the latter. The infraorbital foramen is relatively larger in the *Zalophus* than in *P. hispida*, but there is much variation in this item within the two families. Its size in the pinnipeds is an index to the development of the infraorbital nerve, which serves the mystacial pad. The maxillo-naso-labialis muscle, which is the chief mechanism for opening the anterior nares, arises from the maxilla directly caudo-ventrad of the infraorbital foramen. The point of origin is not indicated upon the skull of *Zalophus* nor of most phocids, but it is marked by a relatively deep fossa in *P. hispida*. The only noteworthy feature of the zygoma that has not been mentioned is the apparent fact that in the Otariidae the malar extends to the glenoid fossa, which it does not quite do in the Phocidae. One not infrequently encounters the statement that in the Otariidae the dorsal process of the zygomatic arch occurs definitely craniad of the jugal-squamosal suture, while in the Phocidae it occurs either at this point or a bit caudad. This is a secondary character and the position of the process is attributable to the relative size of the orbit, and hence, of the eye. As usual the zygoma tells little in regard to the masseter muscles.

The molars of the Otariidae are simple and conical, evidently having assumed their present form because of the slight use to which they are put in simply helping to tear fish and similar food, rather than in shearing tough meat and gnawing bone, as is the habit of the fissiped. The molars of the Phocidae are of a more complicated form and have at least two cusps—often more. Presumably the food predilections of all pinnipeds are very much the same, and it is not

only impossible to explain the dental differences between the two families at the present time but in the absence of ancestral remains it is unsafe to theorize on the probable development of the tooth patterns. The dental arch is different in the two families, being narrow in the *Zalophus*, with alveoli almost parallel, while these diverge to a greater extent in phocids, with *Stenorhynchus* occupying an intermediate position in this as in so many other respects. The palatal region is narrow in *Zalophus* and broad in the *Phoca*, while the hamular processes are located far caudad in the former of their position in the latter animal.

In classifications of the Pinnipedia attention is usually called to the presence in otariids and the absence in phocids of the alisphenoid canal, mediad of the glenoid fossa, for the passage of the external carotid artery. This is a convenient character for classification but is not necessarily a precise criterion, for in the skull of a fur seal (*Callorhinus alascanus*, No. 237266 U.S.N.M.) this canal is present upon the left side but absent on the right. In *Zalophus* the foramen rotundum (for the maxillary nerve) is just craniad of this canal, and in the *Phoca*, mediad to the anterior part of the glenoid fossa. Next caudad is the foramen ovale (for the mandibular nerve), and near this, the Eustachian canal. The apparent position of the stylomastoid foramen (for the facial nerve) differs in the two animals, but in both it is located as usual between the audital bulla and the mastoid. Ventrad of the basioccipital level upon the medial side of the bulla in the *Phoca* is the carotid canal (for the external carotid artery) and the direction of this is latero-dorsad. In the *Zalophus* this foramen is mostly dorsad of the lateral margin of the basioccipital, and its direction is directly craniad. A probe introduced from the caudal end emerges into sight next to the Eustachian canal. The jugular, or posterior lacerated foramen is next caudad, this being a large fenestration in both, but somewhat more extensive in the *Phoca*. Between this and the condyle is the condyloid foramen (for the hypoglossal nerve), larger in the *Zalophus*, but this difference is not found to be uniform in the other pinnipeds.

The pterygoid fossa is much broader in *Phoca hispida* than in *Zalophus* but the significance of this is not readily interpreted. The irregularity of the surface of the basioccipital in the latter indicates stronger anterior rectus capitis muscles in this animal. In this as in certain other species of phocids (as *Cystophora*) there is a large medial vacuity in the basioccipital, which seems never to occur in otariids. In all eared seals apparently the occipital condyles are relatively narrow, while in the Phocidae they are much more flaring, this being especially pronounced in *Phoca hispida*. The reason for this is evidently that the articulation of the head with the neck has

greater need for mobility in otariids, which is accomplished partly by a reduction in the width of the joint.

The paroccipital processes vary greatly in the degree of their distinctness in pinnipeds. In otariids they are apparently always well defined and continuous, by a crest, with the mastoid processes.

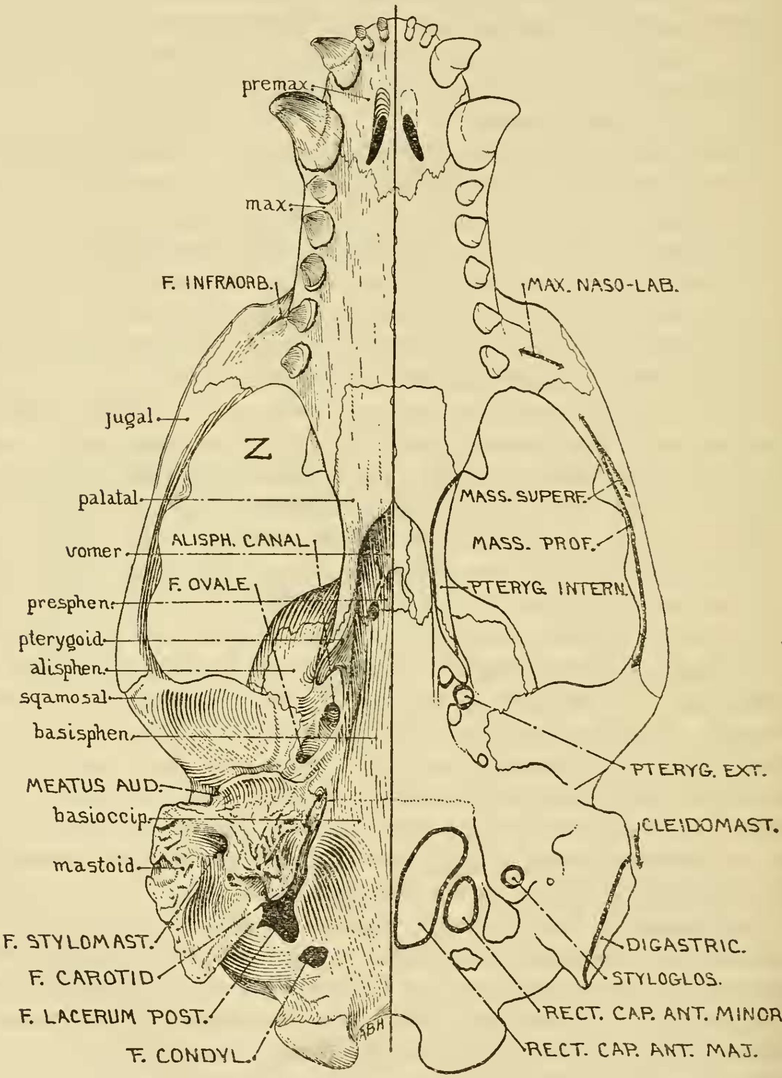

FIG. 4.—VENTRAL VIEW OF THE SKULL OF ZALOPHUS; NAMES OF BONES IN SMALL TYPE

In those phocids in which they are distinct they are never continuous with the latter, but they may be either sharp and projecting (*Monachus*, *Stenorhynchus*), or absent as true processes (*Mirounga*), their position being indicated merely by slight swellings in that part

of the bone. The latter description fits the condition in *Phoca hispida.* In the *Zalophus* the paroccipital-mastoid process begins at the posterior lacerated foramen and extends caudo-laterad. The crest then turns and extends craniad, broadening abruptly and ending as the caudal boundary of the external auditory meatus. Even in the subadult skull there is no indication whatever of a distinct mastoid, it having to all intents disappeared in the parietal-occipital

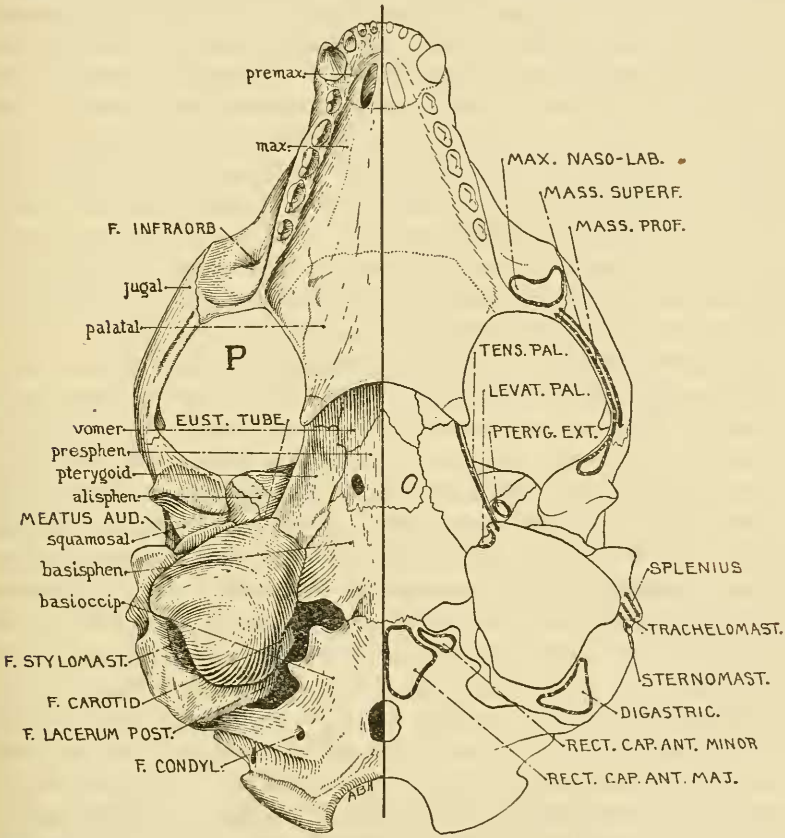

FIG. 5.—VENTRAL VIEW OF THE SKULL OF PHOCA HISPIDA; NAMES OF BONES IN SMALL TYPE

fusion. In *Phoca hispida* there is the slight swelling denoting the position of the paroccipital process, and from this, a lateral bulge of the somewhat inflated mastoid, nonmuscular in character, to the moderately developed mastoid process located caudad of the bony lip of the auditory meatus. As previously inferred, in those phocids which have prominent paroccipital processes there is no continuous prominence from this to the mastoid process. In a fetal *Phoca vitu-*

lina the paroccipital process is much better developed than even a postnatal individual of *Callorhinus*.

If the paroccipital-mastoid crest of the *Zalophus* be viewed as an extension ventrad of the bone, there is little muscular stimulus to be seen—nothing save that of the digastric. If it be viewed as chiefly a lateral development, then there is more reason. In *Phoca hispida* none of the long muscles is attached to the lateral part of the occipital crest, the three muscles of the mastoid process are narrowly tendinous, and the digastric arises from a pit between the mastoid and bulla. This accounts at least partially for the suppression of the paroccipital process as such in the *Phoca*—for there are no muscles attached thereto—and for the moderate size of the mastoid process, with its three muscles. In *Zalophus*, however, the powerful cephalohumeral, the splenius-trachelomastoid insertion, and the sternomastoid—which always has a significant effect upon its insertion—are attached to the latero-ventral part of the occipital crest, and in addition, the digastric arises all along the paroccipital-mastoid crest. There is no attachment at all confined to the mastoid process in its restricted sense save the weak cleidomastoid.

The audital bulla in otariids is small, shrunken-looking and often rugose, extending to form a projecting lip to the auditory meatus directly ventrad of its orifice. There are certain phocids with an intermediate type of bullae, as through *Monachus* to *Stenorhynchus* and then *Phoca*, the culmination being in *Cystophora* with its great globose bullae: and in phocids the projecting lip of the meatus is situated more caudad. A fundamental difference in the bullae of the two families is to be seen in the fetal state. In a *Callorhinus* skull (length 96 mm.) the bullae are very small, noninflated, with tympanic ring very distinct, and border of the auditory meatus regular and subcircular. In one of *Phoca vitulina* (length 113 mm.) the bullae are perhaps 10 times as large, roundly inflated and with the ecto-entotympanic suture almost obliterated, the two parts combining to form a single evenly rounded surface. A point of great phylogenetic importance is the fact that the border of the meatus is irregular and the bone deeply indented cranioventrad, indicating a phylogenetic difference in the procedure of ossification at this point. This same character, but to a slightly different degree, is seen in very young bears (*Ursus*) although in these there is no apparent ecto-entotympanic differentiation, but it even more resembles that found in puppies (*Canis*). A far different condition obtains in the otter (*Lutra*) or any mustelid which I have examined.

In the fetal *Callorhinus* the mastoid exhibits slight inflation, but this rapidly disappears soon after birth and the bone is apparently solid, and thin save where it projects toward the paroccipital-mastoid crest. A very different condition obtains in *Phoca* (*vitulina*), how-

ever, for in a large fetus the mastoid is almost as much inflated as the audital bulla, and the proportions are found to be much the same as in the adult. This character of inflated mastoid is common, in varying degree, to all the Phocidae. As the functions, if any, of mastoids of different degrees of inflation have never been discovered, it is useless to speculate on the differences encountered in the pinnipeds.

In the fetal *Phoca* skull there is a pair of symmetrical bones, one on either side, bounded by the mastoid, parietal, supraoccipital and exoccipital, and measuring 21 by 10 mm. These are found in those few very young *Phoca vitulina* skulls that are available, but their outlines become obliterated in older animals—even in immatures of medium size. In an adult skull of *Phoca groenlandica*, however, and a subadult of *Cystophora*, these accessory bones can be perfectly traced. They can not be considered as Wormian bones, for they are too symmetrical and too regularly situated. It seems justifiable to consider them as a phylogenetic remnant, comparable to the "reptilian" supernumerary bones of some insectivores. (See Wortman, 1921.) I can not, however, find that their undoubted homologue exists in the skull of any reptile which I have encountered in the literature of the subject, unless they are comparable to supratemporals of such a genus as *Procolophon;* and I am far from convinced that this is likely.

In all adult otariids the temporal muscles reach the sagittal crest and in old males they attain a phenomenal size, as indicated by the development of the crests—in fact far larger than one imagines would be of practical use to an animal with such dentition and with such a diet. In a sagittal direction these fossae extend from the lambdoidal crest to the supraorbital processes. In many phocids (as *Mirounga* and some *Phoca*) these muscles also reach the sagittal crest, but as a rule they are much weaker in this family and do not encroach so far onto the frontals. It may be that no old male of *Phoca hispida* is available, but I have seen none in which these muscles reach the sagittal line. In the skull upon which this osteological study is chiefly based they are far apart and weak.

In fetal skulls the supraoccipital of *Phoca* has a more definite rostral inclination than in *Zalophus*. In adults of the latter genus as well as in some phocids (as *Cystophora*) the supraoccipital plane slopes gradually, but in all phocids the occipital crest exhibits quite a sharp angle in the middle portion of either half. This assumes almost a right angle in the *Phoca hispida*, in contrast to the more even curve of this crest in *Zalophus*. The reason for this is not hard to find, for in the otariid the different muscles of paroccipital-supraoccipital insertion are more or less evenly distributed for the entire

length of the crest, while in *Phoca hispida* they are segregated in the regions of the mastoid process and the medial part of the occipital crest. And the latter is therefore the part that has been pushed rostrad in response to certain muscular stimuli, as will be discussed elsewhere. The part of the skull anterior to the supraoccipital has resisted in varying degree the rostral push of the latter bone, the force of resistance being supplied by the density of the water through which the pinniped moves during locomotion. The result, where marked, may be compared to the first stages of the "telescoping" of certain of the cranial elements, as exemplified to

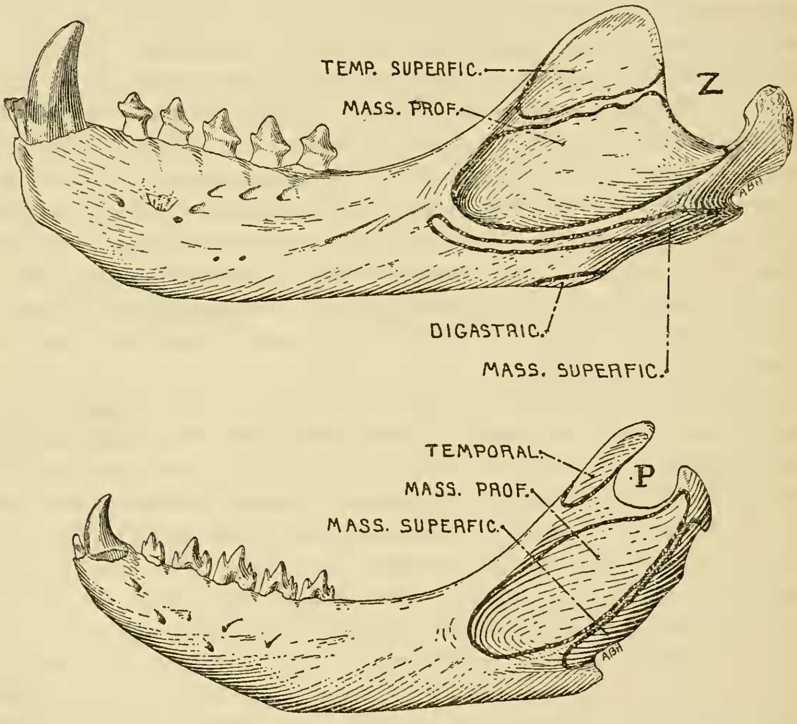

Fig. 6.—Lateral view of the left mandible of Zalophus (Z) and of Phoca hispida (P), showing areas of muscle attachments

such a remarkable degree by the cetacean skull. An indeterminate, though probably small, number of fissiped Carnivora exhibit to some slight extent a sliding movement of the occipital plane, a prerequisite being a squamous, rather than a dentate, type of suture between the bones involved, and some mechanical stimulus is undoubtedly also a necessity. Thus in the skull of an immature *Arctonyx leucolaemus obscurus* (which is supposed to use its nose in digging) with a length of 123 mm. the supraoccipital overlaps the parietals by as much as 8 mm. In the immature skull of an otter (*Aonyx*

cinerea) of 82 mm. the overthrust amounts to 5 mm. A juvenal skull of a *Callorhinus alascanus* of 134 mm. exhibits this condition to an extent as great as 25 mm. It was therefore surprising to encounter in a large immature of *Phoca vitulina* with a skull length of 145 mm. an overthrust amounting to but 8 mm., and this only for 10 mm. upon either side of the sagittal line, laterad to that point it being but a couple of millimeters. Both the otariid and the phocid presumably have encountered, during their aquatic existence, the same or a very similar sort of mechanical stimulus exerted by the water upon the head. It is therefore necessary that the great difference in the amount of this osteological overthrust exhibited by the supraoccipital be accorded phylogenetic significance of great weight.

The form of the mandible is chiefly influenced by that of the skull proper. To conform to the heavier dentition and musculature of *Zalophus*, its mandible is stouter than that of *Phoca hispida.* The coronoid process is very much broader and more suited to the insertion of a large temporal muscle, but relatively the masseteric fossa is about the same in both. The insertion of the superficial part of the masseter is horizontal in *Zalophus* and at an angle of about 45° in the *Phoca*, which variation is at least partly mechanical and due to the fact that in the former the mandible is almost straight, while in the latter it is much curved. This condition has been brought about by the position in the *Phoca* of the glenoid fossa, situated well dorsad of the maxillary tooth row, causing a corresponding position of the mandibular condyle well dorsad of the mandibular tooth row. There is much specific and generic variation exhibited by the mandibles of the two families, however.

HYOID

There is available no adult pinniped skeleton in which the hyoid complex is entirely satisfactory. It is, however, of the usual carnivore type, with basihyal, lesser cornua consisting of short thyrohyal (no chondrohyal was noted), and greater cornua. The latter comprise ceratohyals, adjoining the basihyal, and then in sequence epihyals, stylohyals, and tympanohyal elements, although it is not certain if the latter are completely ossified in all pinnipeds.

VERTEBRAL COLUMN

As previously mentioned, the sum of the thoracic, lumbar, and sacral series of vertebrae is used as a standard with which to compare each series. Unfortunately, no account can be taken in the cleaned skeleton of the thickness of the intervertebral disks; but after all, what is desired is just *some* standard for comparison. The column

of *Zalophus* comprises 44 vertebrae and of the *Phoca* 45,[2] which seems to be a greater number than is possessed by most pinnipeds because of the numerous caudals. It is, of course, almost impossible to decide whether there has been any actual lengthening of the pinniped vertebral column in relation to general body mass. There seems to be a tendency toward lengthening of the thorax in the Otariidae at least, but the lumbar length of fissipeds is entirely too variable for one to make comparisons in this series. Outstanding details of the vertebral column are the slight development of the spinal processes in phocids, highest in the extreme anterior thoracic series of otariids; the thickness and evidently great elasticity of the intervertebral disks, especially in the cervical and lumbar region of otariids; and the osteological provision, also especially in the otariids, to allow for extreme mobility of the individual vertebrae, the pre- and post-zygapophyses being reduced and also all bony details that might collide with an adjoining vertebra during contortive movements. The nomenclature used for the vertebral processes is that most often employed (see Howell, 1926), save in the case of the diapophyses. It is perhaps wise to employ this term only for such inferior processes when they arise from the neural arches, terming them parapophyses when they arise from the centra. I do not pass upon the propriety of this course but follow it for the reason that it conforms to embryological evidence. The investigation of the variation in the back musculature from a comparative standpoint is one that takes a high order of specialization on the part of the investigator, and until some qualified person shall have done this the homolgy of the vertebral processes must be considered as not unassailably established.

Cervical vertebrae.—The cervical series numbers seven as usual. In the *Zalophus* it measures 24 and in the *Phoca* 26 per cent of the body length (27 in a cat). That this difference is so slight is rather surprising, for with its apparently longer body, the otariid appears to have a much longer neck; but the difference is increased during life by the considerably greater thickness in the former of the intervertebral disks. Although the cranial articular facets in *Zalophus* are relatively much narrower than in the *Phoca*, to allow for greater freedom of movement in the former, the transverse processes are somewhat broader and directed more ventrad, a condition attributable in part to the greater complexity in this otariid of the longus colli. To this stimulus is also partly due the differences shown by the more ventral of the vertebral processes. The axis in both animals has a very small process which seems to be an anapophysis. In the *Zalophus* the third cervical shows ventrad only the parapophysial

[2] See p. 22.

plate, with the suggestion of two processes upon its caudal and one upon the cranial termination. In the fourth the cranial has disappeared, or rather is undifferentiated from the remainder of the plate, but the two caudad are more distinct, the superior being directed farther dorsad. In the fifth this has become a distinct anapophysis, separate from the papapophysial plate. In the sixth this condition is much more pronounced and the robust caudal termination of the parapophysial plate exhibits a separate center of ossification. In the seventh, partly because this is the first vertebra lacking a lateral vertebral canal, the inferior process, which is a true process and not a plate as in those more craniad, is situated more dorsad, where it should be considered as a diapophysis. It also has an anapophysis like the sixth. Metapophyses are lacking in all. Conditions are somewhat similar in the *Phoca* with the exception that there is little tendency for the parapophyses to be platelike, save the sixth as usual and in the seventh the anapophysis and diapophysis have virtually fused. In the *Zalophus* there is a gradual increase in the height of the neural spines from the third to the seventh, the latter being 53 mm. in height above the neural canal, while in the *Phoca* there are really no spines upon the last five cervicals, that of the seventh measuring but 12 mm. in height.

Thoracic vertebrae.—The thoracic series of vertebrae normally constitutes 15 in all pinnipeds except *Odobenus*, in which there are 14, for out of 47 individuals of 14 species and genera, of both orders, Thomson (1909) encountered but 1 with 14 thoracics; so Flower (1876) was mistaken in his statement that *Phoca* has but 14. In *Zalophus* the series constitutes 67 per cent, and in the *Phoca* 57 per cent of the body length (46 in a cat). Hypapophyses are distinctly present in the first four and the fifteenth, the latter especially pronounced in the otariid. The neural spines gradually decrease in caudal sequence from the first, which is of about the same height as in the seventh cervical, and they exhibit no pronounced anticline or change in direction, as they do in most carnivores, nor any abrupt change in character, although there is a gradual broadening of the spines. As far caudad as the eleventh vertebra in *Zalophus* the articular surfaces of the zygapophyses are horizontal. Those between the eleventh and twelfth and thereafter (including the lumbars) become progressively more vertical, but the significant feature in this animal is that in all posterior to the first few the two postzygapophyses of each vertebra are exceedingly close together, theoretically allowing of great freedom of movement. In the posterior thorax, however, there is such interlocking of the zygapophyses that a very concave outline of the dorsum can not be assumed, but the convexity, especially in the lumbar region, is only limited in degree by the elasticity of the intervertebral disks.

In the *Phoca* the spines, especially caudad, are but little more pronounced than the other processes. The change in the direction of the articular surfaces of the zygapophyses between the eleventh and twelfth thoracics as mentioned for *Zalophus* is much more abrupt and especially caudad and in the lumbar region the zygapophyses of each vertebra are situated much farther apart—relative to size, over three times farther. The interlocking is such as not to prevent as marked concavity in the outline of the dorsum as the limitations of the sternum will permit, but it is impossible in the cleaned skeleton to judge of the amount of convexity that is possible. This seems to be not so great in the case of the phocids, however.

The transverse processes of the first 11 thoracics in *Zalophus* consist merely of blunt protuberances above the costal facets. They embody, however, met-, an-, and possibly diapophyseal elements, which begin to separate in the twelfth. Metapophyses are of increasing distinctness in the thirteenth, fourteenth, and fifteenth, but anapophyses are absent upon the fifteenth thoracic. There are certainly no diapophyses to the posterior thoracic vertebrae of *Phoca* and a small but sharp anapophysis is present upon the fifteenth; otherwise the lateral details of the two genera are very similar. The first 10 ribs of *Phoca* have both capitular and tubercular attachment to the vertebrae, and of the remaining 5, capitular only. Because of the poorer definition of the facets in the *Zalophus* skeleton (disarticulated) these details could not be determined with certainty, but because of vertebral similarity I judge that the costal conditions are the same.

Lumbar vertebrae.—Unfortunately the *Zalophus* skeleton had but four lumbar vertebrae and the one of *Phoca hispida* three. Thompson (1909) ascribes to Barrett Hamilton a statement that "in most seals the numbers of thoracic and lumbar vertebrae appear to be usually 15 and 3, more rarely 14 and 6." The above figure 3 is probably a misprint for 5, and with this exception I can find no published statement of any otariid or phocid with less than five in this series, while the number appears always to be six in *Odobenus*. It therefore seems justifiable to assume that one lumbar vertebra from the *Zalophus* and two from the *Phoca* have been lost and to compute the lumbar length on the basis of five vertebrae. In *Zalophus* this computed item was 22 and in the *Phoca* 26 per cent of the body length (46 in a cat), and yet in proportion to general body mass the lumbar series seems relatively the longer in *Zalophus*. On the whole these vertebrae are of the same character as the more caudal of the thoracic series save that there are no vestiges of anapophyses and the inferior processes consist of broad parapophyses, relatively much better developed in the phocid. In conformity with the previously mentioned fact that in the latter the zygapophyses are much farther

apart transversely, the metapophyses are also farther apart. In both there are hypapophyseal keels to all the lumbars.

As previously mentioned the outstanding character of the vertebral column as a whole is the looseness of the articulations. The cat is looked upon as being rather a limber mammal, but its vertebrae are far more securely interlocked than are those of the pinnipeds.

Sacral vertebrae.—The sacral series in the pinnipeds is almost always three, although Flower and Lydekker (1891) say four. In all of the 47 individuals of divers sorts examined by Thomson (1909) there were three, as there is in my *Zalophus* skeleton, but in the *Phoca hispida*, a *Phoca groenlandica* in the National collection, and apparently always in *Odobenus*, they number four. In *Zalophus* they constitute 11 and in the *Phoca* 14 per cent of the body length (8 in a cat), but this detail is of but slight value because of the difference in the two in the number of the sacrals. In the *Phoca* but not the *Zalophus* the postzygapophyses of the last lumbar and prezygapophyses of the first sacral are so shaped as to allow the whole sacrum, and thus the pelvis, to be elevated above the general vertebral axis, bowing the back concavely at this point. The specimens available had the articulation of the pelvis with the sacrum confined to the first sacral except in *Odobenus*, in which the first three sacrals were involved.

The only lateral processes in addition to the "transverse processes" are poorly developed metapophyses. In the *Zalophus* the width of the vertebrae decreases regularly from the first to the third. In the *Phoca* the greatest width of the first is considerably greater than in *Zalophus*, to allow for the broader apaxial musculature, and there is then a rather sharp constriction in width of the second. The transverse processes of the third and fourth, fused into a single plate, are again much broader, and the variation in this item must be due to some detail of the sacrospinal musculature that was not detected, for there is no difference in the origin of any of the hip or thigh muscles sufficient to account for it.

Caudal vertebrae.—Flower and Lydekker (1891) give the number of caudals as from 9 to 15, while Thomson (1909) says that in 47 individuals of 14 sorts of pinnipeds there were between 10 and 12. In a single mounted *Monachus tropicalis* there are apparently 13, and in a *Phoca fasciata* of the National collection, at least 14, with the possibility that the terminal ossicle of the tail has been lost. Although possibly unusual, it is therefore not startling to find that there are 14 caudals in both *Zalophus* and my *Phoca*, these bones constituting respectively 24 and 35 per cent of the body length. In the *Phoca* the transverse processes of the more cranial vertebrae are broader, and the spinous processes are lower and broader craniocaudad.

THORAX

Sternum.—In essential features the sternal complex of *Zalophus* and *Phoca* are largely similar. In these two skeletons all of the elements are articulated and the bony portions (exclusive of presternal and xiphoid cartilages) constitute in *Zalophus* 56, and in the *Phoca* but 37 per cent of the trunk length (41 in a cat). In the *Phoca* skeleton there is a long, slender presternal cartilage which is two and a half times the bony part of the sternum and 71 per cent of the whole manubrial complex. In the *Zalophus* a similar result has been attained but chiefly by anterior extension of the bony part of the manubrium. Thus, in the *Zalophus* the latter is 22 per cent (17 in the *Phoca*) of the bony sternum, but the presternal cartilage is insignificant, and but 30 per cent of the size of the manubrium proper. The presternum of *Phoca* projects relatively farther forward than in the otariid, however. The bony manubrium is longer in the latter (over twice the length of the first sternebra), but in both the first pair of costal cartilages arises from lateral processes, in the *Zalophus* caudad and in the *Phoca* rostrad of the middle of the bone. In the former there are six and in the latter seven sternebrae. In the *Zalophus* only, the last of these has a pair of broad facets for the attachment of the costal cartilages. In this genus the xiphoid or enciform bone is relatively shorter but its cartilage is longer than in *Phoca*.

Ribs.—As already mentioned, there are 15 pairs of ribs in both animals, which is normal for otariids and phocids, but *Odobenus* has only 14. Attachment to the vertebral column of the first 10 pairs is both capitular and tubercular, and capitular only in the case of the last 5. The relative stoutness and shortness of the first rib is more accentuated in the *Phoca*. In *Zalophus* the first eight pairs of costal cartilages are securely attached to the sternum, while in the *Phoca* there are nine, there being in this genus one more sternebra.

EXTREMITIES

Pectoral girdle.—This is incomplete in the pinnipeds, there being no clavicle. The scapulae of the *Zalophus* and *Phoca* are very different. In the former the supraspinous fossa is two or more times the size of the infraspinous, the coraco-vertebral angle is well defined, and the vertebral border extends definitely caudo-ventrad. In the *Phoca* there is no coraco-vertebral angle proper, this part of the scapula being evenly curved, and to this extent the supraspinous fossa is reduced. The gleno-vertebral part of the infraspinous space (so termed to differentiate it from the more circumscribed infraspinous fossa proper, from which arises the muscle of this name) is much lengthened, giving to the scapula its characteristic sickle

shape. This places the vertebral border almost parallel with the body axis. In the *Zalophus* there is an epiphyseal cartilage all along the vertebral border, in the skeleton under consideration ossified only at the gleno-vertebral end. In the *Phoca* the only present indication of cartilage is the extensive gleno-vertebral projection, becoming more or less completely ossified with age. The degree to which this

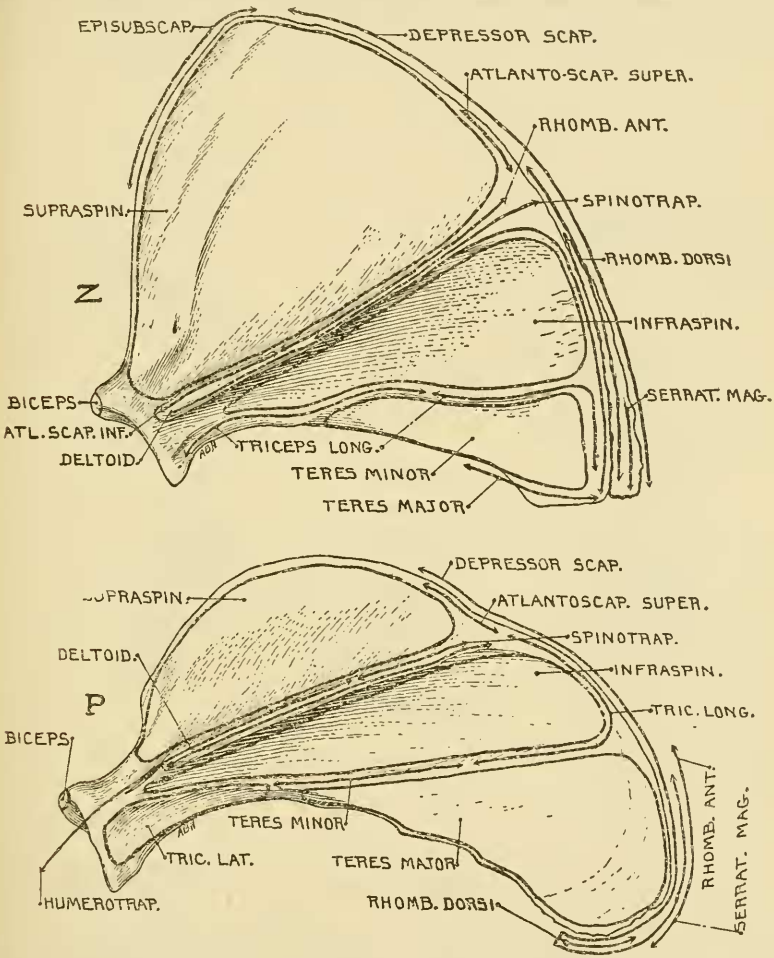

FIG. 7.—LATERAL VIEW OF THE LEFT SCAPULA OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*) WITH AREAS OF MUSCLE ATTACHMENTS

condition obtains within the Phocidae is unknown at present because cartilage often is damaged or disappears entirely during cleaning of the skeletons. In the *Zalophus* the spine, placed not only relatively but actually farther caudad, terminates in a short acromial process, virtually absent in the *Phoca*, but it is difficult to give a myological reason for this difference. There is considerable generic variation

in the scapula. For instance, in *Mirounga* it is nearly of the form more often encountered in the Otariidae, and the supraspinous space is several times as extensive as the infraspinous.

There is such a large number of muscles attached to the scapula that it is impossible to sort out the different myological stimuli, and but a few broad generalities are practicable. The supraspinatus assists in extending the humerus, indicated as being considerably more powerful in *Zalophus.* The true infraspinous fossa, which occupies

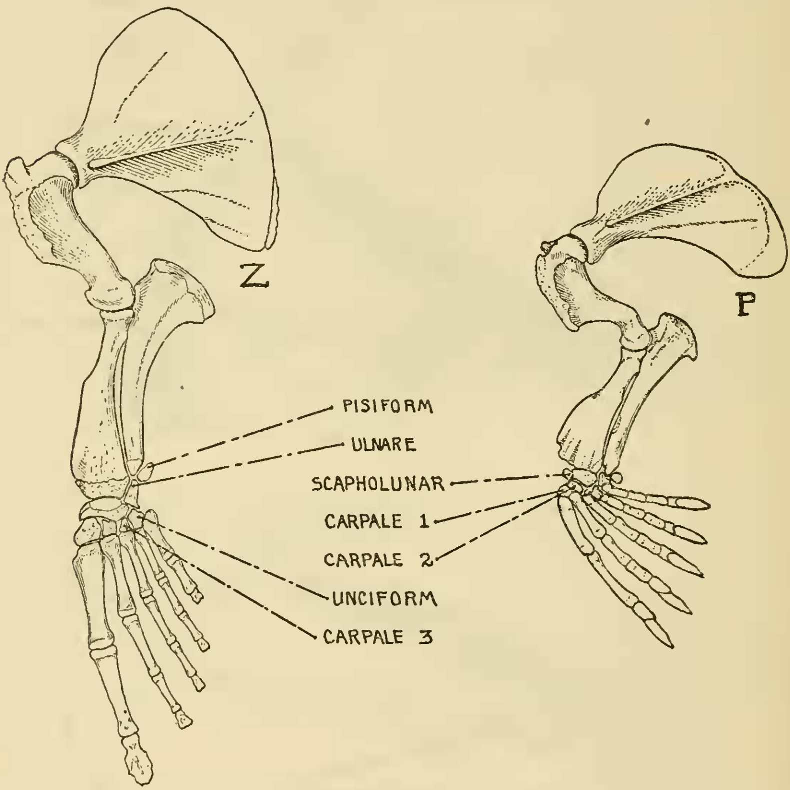

FIG. 8.—LEFT VIEW OF THE ANTERIOR LIMB BONES OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*) IN APPROXIMATE POSITIONS IN WHICH THEY ARE USUALLY CARRIED IN LIFE

about half of the infraspinous space, is more extensive in both animals than the size of the muscle warrants, and it is therefore doubtless in course of becoming still smaller. The infraspinatus is a rotator of the femur, with a slight flexor action in some mammals, but its leverage is small. This function has been assumed in the pinnipeds by the deltoid, which is especially remarkable in the otariids, and with much greater efficiency. Although the triceps is so highly specialized in the Pinnipedia this complex has not been

of prime importance in the modification of the scapula, and the long division in *Phoca* has not even taken full advantage of the extension of the gleno-vertebral angle. In fact, the rhomboids and serratus magnus, rather than any muscles more intimately of the shoulder girdle or brachium, have been chiefly instrumental in this gleno-vertebral extension. In *Phoca* the "teres major fossa," occupying the more caudal division of the infraspinous space, is large; in *Zalophus* it is much smaller and occupied by the origin of the teres minor, while the teres major has been segregated upon the border of the bone adjoining the angle, with limitations well defined osteologically. Between the teres fossa and the infraspinous fossa proper is a slight ridge, occupied in *Zalophus* exclusively by origins of triceps divisions, and in the *Phoca* by the teres minor also. In neither animal is there a true coracoid, but only a faintly indicated bicipital process upon the cranial margin of the glenoid fossa, from which arises the biceps. The angle of the scapular spine in relation to the glenoid fossa is the same in both.

ANTERIOR LIMB.—In the Pinnipedia the functional length of the arm is so termed only because I am using this standard of comparison in the investigation of other mammals, and it signifies merely such a standard. Because most of the arm is within the body, and, furthermore, because in the *Zalophus* there are cartilagenous extensions of the digits, this functional arm length, so termed, bears an unknown relation to the effective lever power of the forelimb, which is discussed elsewhere. This length of arm then, which is of great value from a phylogenetic viewpoint, consists of the distance from the tip (exclusive of the nail in *Phoca*) of the first digit to the proximal termination of the radius, plus the length of the humerus, from trochlea to head. In the *Zalophus*[3] this comprised 66 and in the *Phoca* 48 per cent of the body length (82 in a cat); or, expressed differently, relative to body length, that of the *Phoca* was about 72 per cent as long as in *Zalophus*, a disparity still further increased during life by the presence in the otariid of cartilagenous extensions upon the digits.

Upper arm: *Humerus*.—In the *Zalophus* the humerus comprised 27, and in the *Phoca*, 30 per cent of the arm length (38 in a cat). Because of the disproportionate length of the manus in the former animal this comparison is not as significant as is the humero-radial comparison, which in the otariid was 95 and the phocid 104 per cent. Of the body length the humerus comprised 18 and 14 per cent, respectively (31 in a cat). The articular surfaces of the *Zalophus* are the more robust, relatively, and the fact that the normal position

[3] The manus and pes were disarticulated in the *Zalophus* skeleton, and the measurements computed after reconstruction upon sheets of modeling clay. They were not disarticulated in the *Phoca*.

of the humerus to the scapula is one of greater flexure in the phocid is shown by the position of the head, which in this animal was directed

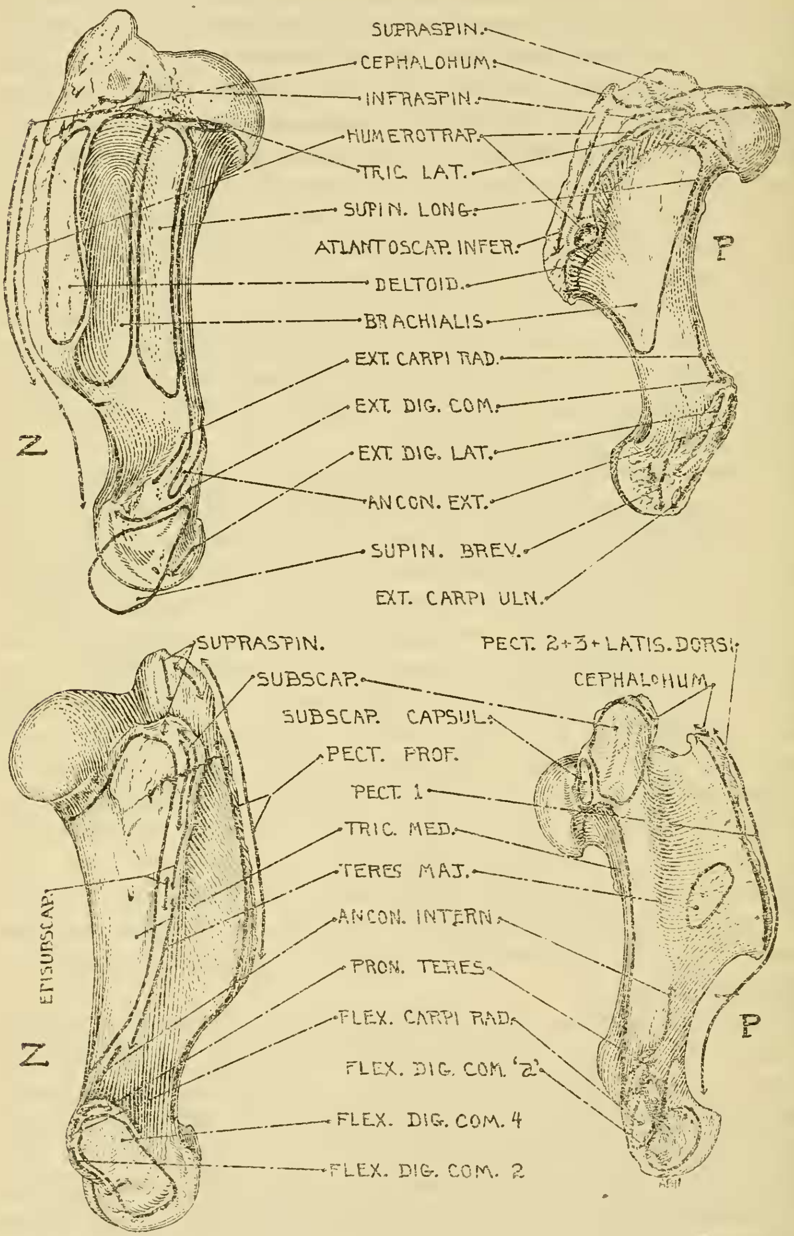

Fig. 9.—Left humerus of Zalophus (*Z*) and Phoca hispida (*P*); in lateral view above and medial below

more caudad of the shaft. The normal angular interrelationship of the different segments is indicated as nearly as possible in Figure

8. Except in shortness, the only way in which the two humeri show a marked resemblance is in the enormus development of the deltoid crest.

In the *Zalophus* the greater tuberosity is very massive and rises well above the head in an irregularly rounded knob, and distad it is prolonged into the broad deltoid crest, which extends for more than half of the shaft, and is raised from the shaft by a relatively thin wall of bone, which in the *Phoca* is thicker because of the lesser depth in that animal of the fossa from which arises the brachialis. In the *Phoca* the greater tuberosity is no higher than the head and the part adjoining the latter is relatively narrow, while there is a projection of bone stretching toward the lessor tuberosity, between which there extends a stout ligament as in many carnivores. The deltoid crest is relatively broader than in *Zalophus*—almost as broad as the shaft—the borders are more overhanging, and the distal termination extends no farther than the middle of the shaft. Upon the lateral border is a pit, of varying definition individually, for the reception of a separate tendon of the humerotrapezius. The only striking difference in muscle insertions that might account for the variation of the greater tuberosity is the much larger supraspinatus in *Zalophus*, but the chief reason is undoubtedly the different sort of work, and at a different angle, that the muscles of the two animals need to perform. The greater height in the otariid would allow of more powerful extension of the humerus. And the farther extension distad of the deltoid crest in this animal provides a greater leverage for the deltoid and pectoralis. In the *Zalophus* the lesser tuberosity, placed mediocraniad of the head, is very much lower than the head, but is massively rounded and its base gradually merges with the shaft. In the *Phoca* the homologue of the lesser tuberosity is phenominally developed, somewhat falciform, and higher than either the head or the "greater" tuberosity. Its base assumes more the form of a ridge. To account for these differences there is ample muscular variation. The subscapularis is of course inserted upon this tuberosity and it is evidently much better developed and hence more powerful in the phocid. In this animal a portion of the cephalo-humeral and the ligament between the tuberosities probably account for the falciform part of the lesser, while there is also insertion of the small subscapulo-capsularis, absent in the otariid, but the latter has the episubscapularis, which the phocid lacks. In final analysis, however, it is impossible to say that the diametrically opposed conditions of the two tuberosities in these two animals are due to this or that muscle.

The bicipital groove lies between the two tuberosities and this is relatively much the more capacious in *Phoca*. Within its channel, just proximad to the middle of the shaft, lies the teres major rugosity,

absent in *Zalophus*, for in the latter this muscle inserts narrowly upon the extended base of the lesser tuberosity. Just below the head in *Phoca* is a definite ridge, this being in line with the proximal extension of the entepicondylar ridge which marks the origin of the supinator longus. In *Zalophus* this origin is much more extensive and there is no ridge. In *Zalophus* the lateral epicondyle projects hardly laterad of the trochlea, but much more in *Phoca*, while in *Zalophus* the medial epicondyle is greatly developed and slightly so in the phocid. The only explanation which can be offered for these conditions is the inference that in the otariid the flexors of the lower arm, some of which arise from the medial epicondyle, are considerably more developed as regards angle of leverage and, therefore, effectiveness, than the extensors; and the flexors are the ones needed for powerful backward thrusts of the flippers in swimming. In the *Phoca*, however, it appears as though the stimulus for the development of the extensors has been at least as great as in the case of the flexors. The extensors are used in such motions as upward thrusts of the manus to assist in submergence or depressing the anterior part of the body. The *Phoca*, but not the *Zalophus*, has an entepicondylar foramen; but this is not a uniform character distinguishing the two families, for Thomson (1909) examined a number of skeletons of seven species and genera of the Phocidae in which this faramen was absent.

Forearm: *Ulna.*—Although the ulna of *Zalophus* appears the more massive, the greatest length of this bone is 123 in the otariid, and 131 per cent in the phocid (114 in a cat), of the articular length of the radius. The chief feature of this bone in the pinnipeds is its broadness proximad. In *Zalophus* the lesser sigmoid cavity is relatively deeper and the coronoid higher. A well-defined ridge occurs upon the lateral surface, separating the origins of the extensores metacarpi pollicis radiad, and the pollicis longus ulnad, the latter being about half the size of the former. In the *Phoca* the last-mentioned muscle occupies but a very restricted area near what is termed the ulnar process of the olecranon. This is considerably more falcate than in the otariid. Extending in *Phoca* from the radial process of the olecranon to below the sigmoid cavity is another small ridge, marking the insertion of the anconeus extrenus, but this ridge does not occur in the otariid and the muscle inserts by fascia upon the posterior border of the olecranon. Instead, there is a ridge farther radiad, marking with greater sharpness in this animal the lateral boundary of the triceps medialis. Just distad of the middle of the shaft from the lateral aspect there is a pronounced rugosity in the phocid but not the otariid, and in the former a corresponding one adjoining upon the radius marking a restricted but very strong

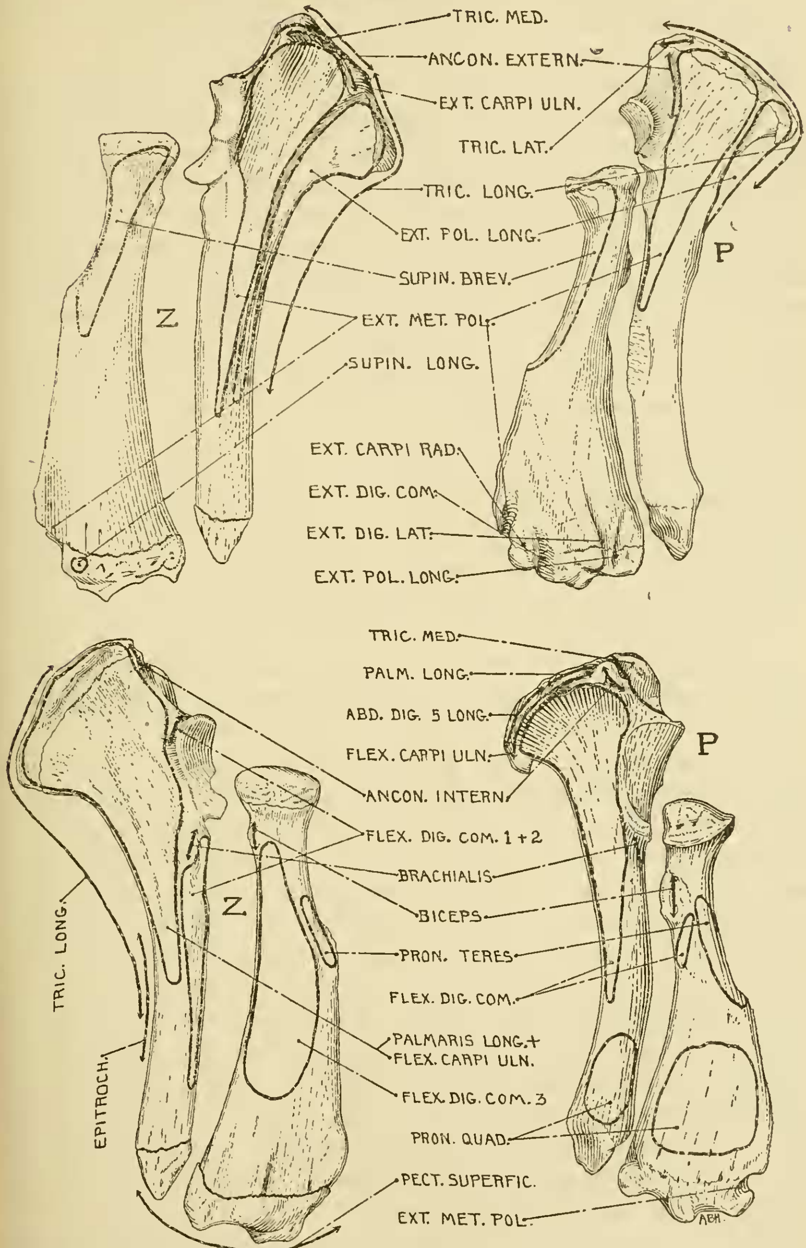

FIG. 10.—LEFT RADIUS AND ULNA OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*); IN LATERAL VIEW ABOVE AND MEDIAL BELOW

interosseous ligament, which occurs in *Zalophus* as the more usual and extensive interosseous membrane with little or no osteological indication. There may, however, be considerable variation in this detail.

The medial or flexor surfaces of the ulnas of the two pinnipeds are very similar, save for the relatively greater area proximad in *Zalophus*. In this animal practically all of this area is occupied by the origin of the very greatly specialized palmaris longus, and in the *Phoca*, by the second head of the flexor digitorum communis. Distad of the coronoid is the rugosity marking the insertion of the brachialis tendon, and still distad along the radial border, a slight crest in *Zalophus* only for the second head of the flexor digitorum communis. There are slight differences in the distal head of the ulna of the two animals, conforming to variation of the articular surfaces of the adjoining bones.

Radius.—In the *Zalophus* and *Phoca* the radius comprises about 20 and 14 per cent, respectively, of the body length (30 in a cat), 29 per cent in both of the arm length (36 in a cat), and 105 and 96 per cent, respectively, of the humeral length (104 in a cat). The most significant feature of this bone in the pinnipeds is the great expansion of its distal half. In the *Phoca* the bicipital rugosity is much the better developed, and there is also a well-marked rugosity for the interosseous ligament, absent as such in the *Zalophus*, as previously mentioned. The proximal part of the shaft is almost cylindrical, but at the center in the phocid and proximad thereto there is a pronounced expansion and process upon the radial side, which I have termed the "pronator teres process" because it is covered by the insertion of that muscle. The muscle, however, did not include any pronounced tendon or other feature which I considered would logically bring about the development of such a well-defined process. In *Zalophus* there are upon the flexor side of the distal part two broad, shallow grooves for two groups of flexor tendons, and upon the radial part of the extensor side, another for the extensor metacarpi pollicis tendon. Upon the flexor side in *Phoca* there are no grooves at all, but upon the extensor side these are numerous and deep. (See fig. 10.) This would seem to indicate that in the *Phoca* the somewhat specialized function of the extensor is in powerful recovery of the manus after flexion; which is in entire accord with the theory advanced partially to account for the greater phocid development of the lateral epicondyle of the humerus.

Hand.—The length of the manus, osteologically (not including terminal cartilage in the otariid nor the nail in the phocid), comprises 29 per cent of the body length in *Zalophus* and 19 in the *Phoca* (21 in a cat), while it measures 44 and 41 per cent, respectively,

of the length of the arm. From a functional standpoint this is not accurate, as the effective area of the manus in the eared seals is augmented by a considerable cartilagenous extension of the digits.

The nomenclature of the carpal and tarsal bones herein employed has been adopted after due deliberation, and is made up from the three methods of terminalogy (see, for instance, Flower and Lydekker, 1891, pp. 49 and 52) usually used in the cases respectively of the simpler reptiles and amphibians, in mammals in general, and third, human anatomy. Those terms are used which it is felt that the student who has not specialized in anatomy will most readily grasp and remember. The carpal elements, then, consist of scapholunar, ulnare, first, second, and third carpales, unciform and pisiform.

The proximal articular surfaces of the scapholunar and ulnare, and of the metacarpals of *Zalophus* extend slightly farther dorsad than in the *Phoca.* This, clearly, has been brought about by the usual position of the forefoot when the animal is on land, the otariid resting the anterior portion of the body upon the carpus, with the digits at a right angle to the forearm; while such a position is more rarely, and perhaps less decidedly, assumed by the Phocidae. In *Zalophus* the scapholunar is perhaps of unusual size, largely because of the great distal width of the radius. Carpale 1 is very large, probably not so much because it is primitive (Gregory, 1910) as that it has need to conform in size to the stoutness of the first metacarpal. Carpale 3 is the smallest of this series but is not pyramidal in form, and there is broad contact between the scapholunar and the large unciform. The pisiform occupies the angle between the radius and ulnare. The proximal extremeties of the first four metacarpals are approximately on a line, but that of the fifth is located markedly more proximad, articulating mediad with the unciform and to a very slight extent with the ulnare. The metacarpals do not lap one over the other, but there is an extensive articulation between the heads of the second and third.

In the *Phoca* there has been considerable reduction in the size of the carpus, and alteration in the relationship of the elements so as to allow excessive abduction of the manus. Carpale 1 is moderately large, but perhaps not when one considers the greater robustness of the pollex. The proximal end of the first metacarpal, however, is distad of the level of the middle three; in fact in dorsal view the proximal end of carpale 1 and of metacarpals 2, 3, and 4 are upon the same level. Carpale 1 reaches the scapholunar upon the palmar aspect but not dorsad, for between there is interposed carpale 2, which has broadened and lies between the first carpale and metacarpus two on the one hand, and the scapholunar upon the other. The second carpale is thus invisible from the palmar aspect; and the unciform is also much smaller from this view than it is dorsad, while

carpale 3 is markedly pyramidal, in palmar view being large and dorsad appearing as a restricted bony point. In the *Phoca* also the articulation of digit 5 with the unciform is upon the lateral side of that bone and considerably proximad of the level of articulation of the three middle digits. There is this difference, however; whereas in *Zalophus* the articular surface of metacarpus 5 is mediad, allowing the digit to point straight distad, in the *Phoca* it is proximad as in the other digits, and the fifth therefore is inclined to point laterad, making this digit, in fact, very much more "opposable" than is the pollex. The explanation for the narrow carpus in *Phoca*, and for the movement distad of the first digit and both proximad and laterad of the fifth, is probably that in the phocid the motions performed by the manus during swimming are of a pivotal, paddling type, much as are those of man when he is maintaining a static position in the water by means of his hands alone. The explanation for the movement distad of the pollex and both proximad and laterad of the fifth lies probably in the extreme amount of abduction of the manus in relation to the antibrachium, of which this pinniped is capable. In an articulated manus of *Monachus tropicalis* there is even more pronounced abduction in the normal position of the fifth digit, the first carpale is several times the size of the second, but the latter does not completely separate, in dorsal view, the first from the scapholunar.

In both animals the pollex is the longest digit and there is sequential reduction in length to the fifth, although this is much more pronounced in the *Zalophus*. In the latter the first metacarpal is much the longest and very much more robust than the others, and it is sharply flattened upon its medial border, possibly to assist a streamline form of the external surface of the flipper. In this animal it is slightly longer than the first phalanx of the same digit, while in the phocid the reverse is the case. In the otariid the fifth digit is much less robust than the first, but more so than the other three, while the third is a trifle the most slender. There is present a decided tendency toward the flattening of the digital elements which in the *Phoca* is encountered only to very slight degree in the pollex alone. Kukenthal (1890) reported indications of double epiphyses in the phalanges of the manus of several pinnipeds, both otariid and phocid. Such may be the case, but they are not convincing in the material at my disposal. In *Zalophus* the terminal phalanges are flattened and distorted in characteristic fashion and contain pits for the rudimentary nails. In the *Phoca* the broad, well-developed nails are retained in the cleaned skeleton.

Pelvic girdle.—There are fundamental differences of a very interesting character existing in the innominate bones of otariids and phocids. The practical comparison of their measurements is rendered difficult, however, by the fact that in the earless seal the ilium

is bent laterad almost at a right angle to the remainder of the complex. The total innominate length in *Zalophus* is 21, and in the *Phoca* 26 per cent of the body length (25 in a cat) ; but the significant comparison is of the part craniad of the anterior lip of the acetabulum

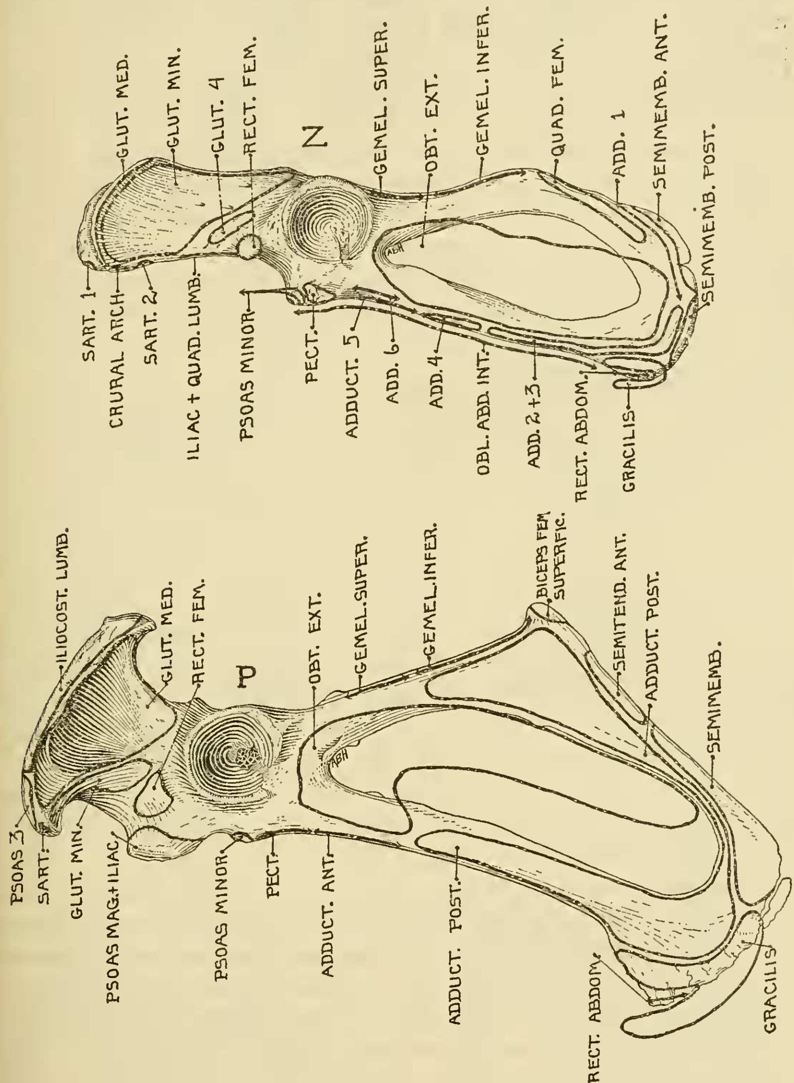

Fig. 11.—Left innominate bone of Zalophus (*Z*) and Phoca hispida (*P*)

with the portion caudad of the posterior lip. In the *Zalophus* this iliac part is 32, and in the *Phoca* but 16 per cent of the innominate length (59 in a cat), while a comparison of the pubo-ischiac portion gives a percentage respectively of 55 and 74 (33 in a cat). An analysis of these conditions is presented farther on. The sharp bend

laterad of the ilium in the *Phoca* has been caused chiefly by the iliocostalis portion of the back musculature, attached to almost the whole anterior (or "medial") face of the bone. As the femur is very short in this order, there is no need for a long ilium or long leverage for the flexors of the thigh. In both animals the insertions of the muscles extending from the posterior innominate to the knee and shank have migrated distad, and in order to increase the lever arm, there has also been a lengthening of the ischium and pubis. Why this should be marked in *Zalophus* is not so clear, for the muscles concerned are not of such fundamental importance to that animal; but this increased leverage—so well developed in the *Phoca*—is of basic importance in the adductional movements employed in swimming. In this animal there has also been some extension dorsad of the spine from which arises a part of the biceps femoris, which allows an elevation of the flippers in characteristic fashion, and ventrad of the inferior tuberosity of the ischium, adding to the effective range of movement.

The remainder of the muscular stimuli which operate upon the innominate are so complex and so involved with phylogeny and angles of leverage that a discussion in further detail is hardly justified. There may, however, be mentioned the greater prominence in *Zalophus* of the rectus femoris process, cranio-ventrad of the acetabulum, hardly more than a rugosity in *Phoca*. There is a single psoas-pectineal process in *Zalophus*, represented in *Phoca* by a large psoas magnus process, more cranially and ventrally placed, and a faint psoas minor process more caudad, while the pectineus arises from no prominence at all but has fleshy origin from the border of the pubis. There is no fused symphysis pubis in either animal, but this term is employed for convenience to designate this region; and there is an ischial epiphysis in both, located caudad and probably the more extensive in *Phoca*, but this is difficult to determine in the skeletons available.

Posterior limb.—The length of leg from a functional standpoint is of a questionable degree of value for the reasons not only that all but the pes is within the body covering, but also because the normal and more or less fixed position of the femur is flexed in the *Zalophus* and somewhat extended in the *Phoca*. The length of the hind limb is considered as constituting the sum of the lengths of the femur (head to condyle), tibia, and the distance from the tip of the second toe (exclusive of the nail in *Phoca*) to the posterior part of the astragalinar condyle. In *Zalophus* this is 62, and in the *Phoca*, 74 per cent of the body length (104 in a cat).

Thigh: *Femur.*—In the *Zalophus* the femur is 18 and in the *Phoca* 16 per cent of the limb (33 in a cat); of the tibia, 50 and 40 per cent; and in relation to the body length 11 and 12 per cent, re-

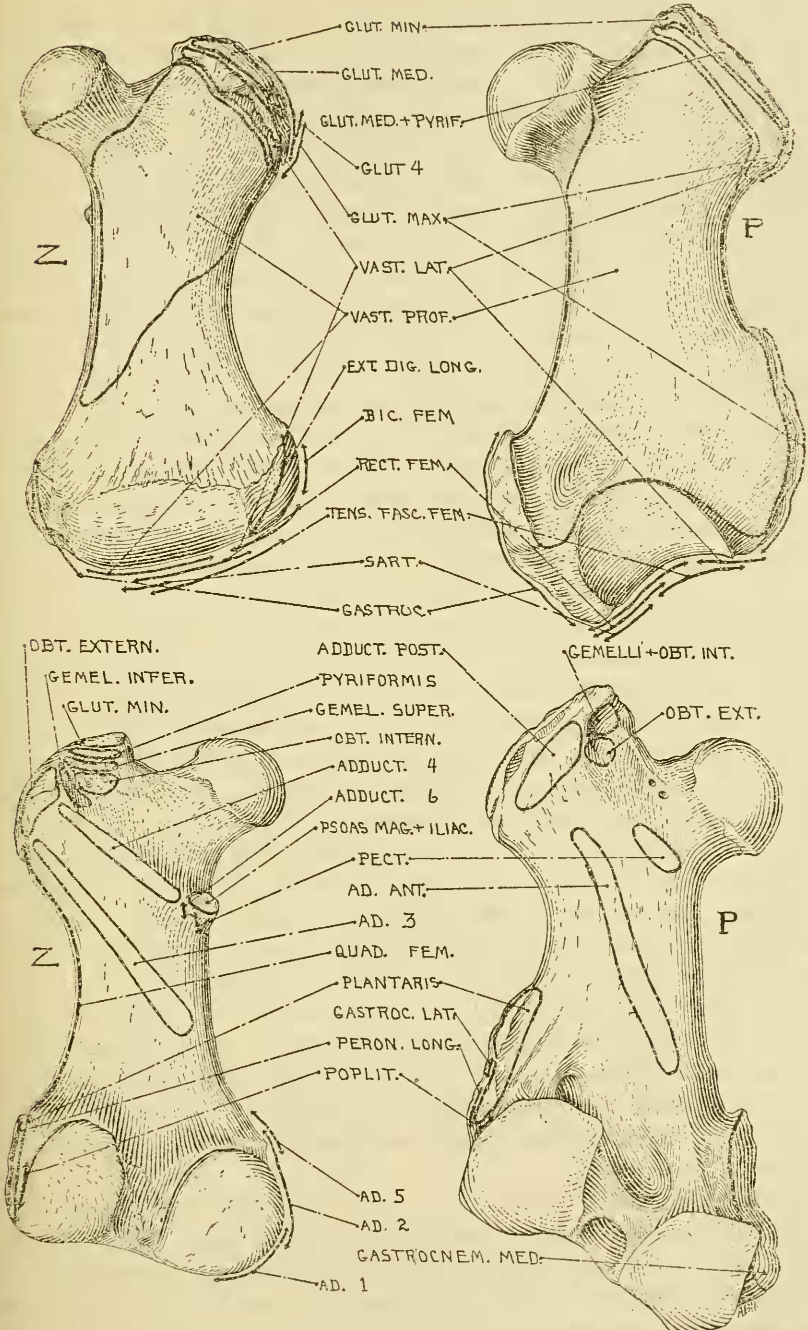

FIG. 12.—LEFT FEMUR OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*); ANTERIOR ASPECT ABOVE AND POSTERIOR BELOW

spectively (35 in a cat). Perhaps the latter comparison is the more significant from a phylogenetic aspect, although this is difficult to decide. In major details this bone is very similar in the two animals. The shaft is expanded laterally, being practically twice as broad in this direction as sagitally. The greater trochanter is laterad of the head and is greatly developed, as high as the head in *Zalophus* and slightly higher in *Phoca*. The summit of this trochanter in the latter is wedge-shaped and there is a deep and distinct trochanteric or obturator fossa, this being due to the tendency toward complete fusion of the tendons of the gemelli and obturator muscles which insert therein. In the *Zalophus* the insertions of all these muscles are separate, the trochanteric fossa therefore being less well defined and nothing but a shallow groove, reaching the summit of the greater trochanter, so that it has the shape of an inverted comma. *Zalophus* has a lesser trochanter, upon which insert the pectineus, adductor 6, and the psoas magnus and iliacus element. The *Phoca* has no indication of a lesser trochanter and in the situation corresponding to its position in the otariid there is only the somewhat extensive and fleshy insertion of the pectineus. From the lesser trochanter to the distal part of the greater there is in the *Zalophus* a slight ridge, marking the insertion of adductor 4, absent in the phocid. In the former the adductor 3, and in the latter the adductor anticus (probably homologous) is inserted in a line passing (approximately) from the medial epicondyle to the greater trochanter. There is in the otariid the suspicion of a ridge marking its location, corresponding evidently to the usual linea aspera. The epicondyles of the *Phoca* are the better developed, being broader, and extending farther proximad more in the nature of definite ridges. This seems to have been influenced by the better development in the phocid of the gluteus maximus, gastrocnemius medialis, and plantaris. In the *Zalophus* the patellar " fossa " is broad and slightly convex, while in the *Phoca* it is narrow and quite deeply concave. This detail varies considerably within the family, but it is probable that in the otariids the patella is never in quite as close relation to the femur as in phocids. In the small *Zalophus* dissected the femur was flexed to such a degree that the patella was situated at the apex of the angle formed by the thigh and shank segments and was almost entirely distad of the femur.

In the otariid the two condyles were of equal size, were directed exactly at a right angle to the shaft, and the outer was sufficiently proximad of the more medial so that a line passing laterad through the center of both would form an angle of about 79° with the axis of the shaft. In the *Phoca* the condyles were directed not quite so far as at a right angle to the shaft, the medial was but about two-thirds the size of the lateral, and a line through their centers would

form an angle of 63° with the axis of the shaft, thus placing the medial much more distad than the lateral. The reason for this will be discussed on page 127.

Lower leg: *Patella.*—The relation of the patella to the femur is discussed in the last paragraph. It is much more conical, especially in the Otariidae, than is the case with most mammals.

Tibia.—In the *Zalophus* and *Phoca*, respectively, the percentage of the tibia to body length is 22 and 29 (36 in a cat); to leg length, 36 and 39; and to the femur, 202 and 200 per cent (104 in a cat). The relative proportions of the thigh to the shank are therefore about the same in both animals. In the *Zalophus* this bone is relatively straight, robust, and with but slight constriction along the middle of the shaft. In the *Phoca* it is more curved and there is a greater constriction in the middle of the shaft. In this animal the posterior tibial fossa is deep and much better defined than in the otariid, and the anterior tibial fossa is but slightly indicated in both. In both the articular surface of the head is slightly altered from its normal position, the lateral part being situated a trifle more distad than the medial, this being more accentuated in the otariid. In the phocid there are nodular growths of bone about the border of the head, indicating some sort of pathologic condition. Distad the astragalar articular surface is much deeper and more cupped in the phocid and the medial malleolus does not project beyond the rest of the bone, as it conspicuously does in *Zalophus*. In the latter the grooves for the passage of tendons are very poorly defined, while in the phocid they are very deep, as they are in the radius. Craniad there is a deep one for the tibialis anticus, and caudo-mediad two, the more medial for the tibialis posticus and the other for the flexor digitorum longus.

Fibula.—The head of the pinniped fibula is solidly fused with that of the tibia and the distal extremeties of the two bones are immovably bound together by ligament. The fibular part of the common head is more or less on a level with the tibial part in the *Phoca* skeleton, but in the *Zalophus* it slopes very sharply distad, in this way providing for an excessive degree of flexion of the knee in this animal. That the condition of this detail is not uniform in the Phocidae is, however, shown by a skeleton of *Phoca groenlandica*, in which there is almost as much of a slope to the fibular head as in my *Zalophus*. The relative position of the heads of the two bones is about the same—perhaps a trifle farther caudad in *Zalophus*—but distad the fibula of the otariid curves quite far craniad, which seems never to be the case in the Phocidae. This changes the position of the ankle joint so that if both animals were normally plantigrade the otariid would toe in to a considerably greater extent than the phocid. The fibular shaft of the former is almost uniformly cylin-

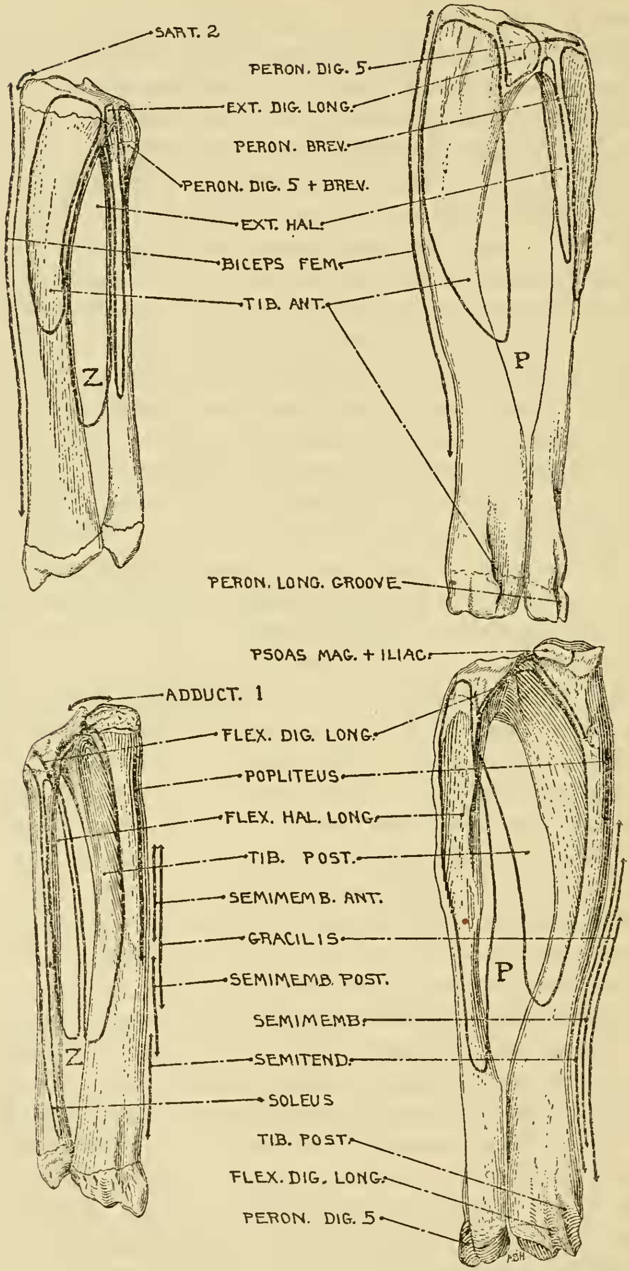

Fig. 13.—Left tibia and fibula of Zalophus (*Z*) and Phoca hispida (*P*); in lateral view above and medial below

drical, while in the latter it tapers from both ends toward the center, and there are two well defined fossae—one cranio-laterad, from which arises the peroneus brevis, and the other caudad, giving origin to the flexor hallucis longus. In the otariid the origins of both these muscles have a somewhat different relationship in regard to the fibula. The distal head of the otariid fibula is rather short, being definitely shorter than is the medial malleolus, relatively smooth and without grooves, and with but slight articulation with the ankle. In the *Phoca* the fibula projects distad of the medial malleolus, its surface for articulation with the ankle is almost as extensive as that of the tibia, and there are two very deep grooves laterad. The more caudal of these is for the peroneus digiti quinti, and the more cranial for the peroneus longus.

Foot.—If the osteological length of the foot for the present purpose be considered as comprising the distance from the tip of the terminal phalanx of the second digit to the caudal part of the condyle of the astragalus, then for the *Zalophus* and the *Phoca*, respectively, it constitutes 28 and 34 per cent of the body length, and 45 per cent of the leg length in both.

The tarsal elements of these two pinnipeds comprise astragalus, calcaneum, centrale, first, second, and third tarsales, cuboid, and a medial sesamoid. The astragalus is especially interesting and exhibits differences of much significance. In the *Zalophus* the position of this bone is slightly more dorsad of the calcaneum, the tibial facet is much larger than the fibular and its slope is more sharply ventrad, in part to compensate for the more distal position in this animal of the medial malleolus as compared to the lateral. This facet extends craniad in *Zalophus* only just onto the neck, and caudad in the *Phoca* only onto the posterior extension of the bone. From the fibular facet there is a broad process extending cranio-laterad, absent in the *Phoca*, and in the *Zalophus*, a constricted neck and expanded head, with an extensive, rounded facet for articulation with the centrale. In the *Phoca* the neck is of greater diameter than the head, and ventrad the articular facet is more extensive, a result of the greater degree of movement possible in this animal. In the *Zalophus* no part of the bone extends caudad of the tibial facet for a greater distance than a couple of millimeters. In the *Phoca* the astragalus is prolonged caudad in a truly remarkable process which extends beyond the termination of the calcaneum and is grooved for the passage of the flexor hallucis longus tendon. It is the tendon of this muscle only and its tension operating on the process of the astragalus, that prevents the foot of *Phoca* from assuming a position at a right angle to the shank.

The calcaneum of *Zalophus* is markedly constricted in the middle, being moderately expanded caudad and greatly so craniad, but that

of the *Phoca* lacks any such constriction. As might be expected from the great caudad development of the astragalus in the phocid the caudal process of the calcaneum is correspondingly reduced in robustness, which is not the case in the otariid. In the latter the anterior and posterior facets (the anterior and middle facets of man are fused in the Pinnipedia) are less extensive than in man, and still smaller in the phocid. Dorsad in the *Phoca* only there are two deep grooves, the more medial for the tendons of the peronei brevis and digiti quinti, and the more lateral for the peroneus longus. In the otariid only the expanded distal portion allows slight contact with the centrale.

The centrale of *Zalophus* is flat in a cranio-caudal direction but broad transversely, while in *Phoca* it is more irregular, is relatively narrow transversely and deep dorso-ventrad, making the narrowest

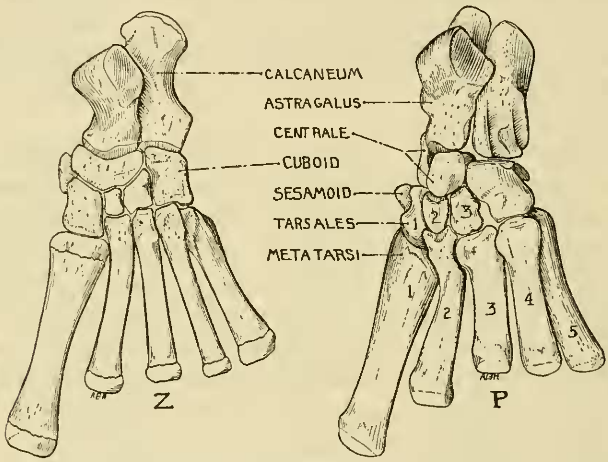

FIG. 14.—DORSAL VIEW OF LEFT TARSUS AND METATARSUS OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*)

part of the tarsus through the centrale-cuboid, while in the otariid it is across the neck of the astragalus and through the calcaneum.

The lateral part of the cuboid is deeply grooved in *Phoca* only, for the passage of the peroneus longus tendon, and the whole bone is not only more irregular in shape, but relatively a bit larger than in the *Zalophus*.

Tarsale 1 is very large, corresponding to the size of the hallux, but lies considerably more laterad (less dorsad) in the *Phoca*. In both animals tarsale 2 is slightly smaller than tarsale 3. Mediad to and fairly between tarsale 1 and the centrale of *Zalophus* is a well-defined sesamoid bone. It is mostly embedded in the tendon of the tibialis posticus but in adults its position is osteologically indicated by small but distinct articular facets upon both bones. In the *Phoca* dissected there was apparently no sesamoid occurring as a real bone,

but in the skeleton studied there was one, relatively as large as in the *Zalophus*, but in contact only with tarsale 1—not with the centrale.

In the otariid the four lateral metatarsals have responded to a transverse crowding and proximad are flattened in this direction, while the large hallux is very much flattened and transversely expanded. The fifth is slightly more robust than the three middle metatarsals. In the *Phoca* there has been equal or greater crowding proximad but the metatarsals have been less responsive, interlock to a much greater extent, and send a number of processes here and there. Another result of this crowding of the tarsal elements is the slight forcing in a plantar direction of the first, and more decidedly of the fifth, metatarsals of the phocid. It is apparent that in the latter there is some decrease in the mobility of the tarso-metatarsal articulations. As with the otariid the fifth metatarsal is slightly more robust than the three middle ones, and the first still heavier, but the difference in size is not so pronounced. In profile the dorsal outline of the metatarsals in this genus is markedly concave, to a conspicuously greater degree in this animal than the otariid.

In both animals the first and fifth digits are longer than the middle three and in the otariid there is a tendency toward flattening of the phalanges. Several investigators (as Kukenthal, 1890) have stated that all except the terminal phalanges of the pedal digits of the pinnipeds show distal as well as proximal epiphyses, in this respect approaching conditions in the Cetacea. As far as my own experience is concerned, there is but one small juvenal *Callorhinus* available which seems to have nodules of bone in the cartilage of the toe joints representing distal epiphyses. All other individuals at hand are sufficiently old so that no line of fusion at the distal ends of the phalanges can with certainty be traced. The middle three digits of the *Zalophus* have well-formed but slender nails, while those of the first and fifth are rudimentary. In otariids there is a terminal cartilage projecting in each pedal digit beyond the nail, and rather scanty material leads me to believe, for the present at least, that these cartilages are relatively longer in juveniles than in the adult. In the *Phoca* the nails are better formed, those of the first and fifth being larger than the other three. They project beyond the tips of the toes, as there are no terminal cartilages in this family.

MYOLOGY

In the following pages the comparisons are based upon the musculature of the *Zalophus* dissected, notations being made upon the muscles of the *Phoca* only when these showed details that differed. Attention is called to points wherein Murie's *Eumetopias* and *Odobenus*, or Miller's *Arctocephalus* and *Phoca* differed from the conditions in the respective families as I found them to be represented by

the animals dissected by me. But in some instances the above authorities—especially the former—omitted reference to certain muscles, or groups of muscles, and in other cases the descriptions were so involved as to be obscure. All details of differences are not given, of course, but only those of sufficient degree or quality to be deemed of some importance. The differences in origin and insertion of a muscle in the two animals are not always as great as indicated in the osteological drawings. Thus one investigator might consider that the vastus profundus (fig. 12) arises in *Zalophus* from only the proximal part of the femur, and in *Phoca*, in which animal there is slightly more tenacious attachment, that the origin is from the entire shaft, although in reality the muscular difference is very slight indeed.

As previously mentioned the *Zalophus* dissected was a juvenile and excessively lean, but its condition of preservation was excellent. The *Phoca*, on the contrary, was very fat and its condition poor, due in part to rupture of some of the blood vessels, especially about the shoulders, and consequent infiltration between the muscles of blood, the caked condition of which made dissection difficult at times. The coloration of the muscular tissue in these preserved specimens was about the same as in the usual fissiped, but it is common knowledge that the flesh of a freshly-killed pinniped, as well as of the Catacea, is unusually dark. As the flesh of the horse is of a similar color, however, this is not necessarily connected with aquatic specialization.

It may not be out of place here to mention that the musculature of the Pinnipedia does not differ as greatly from that typical of the terrestrial Carnivora as one might expect from the osteology, and there were but few times when I experienced any difficulty in readily homologizing the musculature to my satisfaction.

MUSCLES OF THE HEAD

1. SUPERFICIAL FACIAL MUSCULATURE

For the reason that Ernst Huber is making a separate study of the facial musculature of both specimens which I dissected, there will be but four of this group mentioned in the present report, this for the reason that they are intimately concerned with functions which it is wished to discuss.

M. platysma (fig. 15) was extensive in both *Zalophus* and *Phoca* but was not otherwise peculiar.

M. naso-labialis arose mediad of the anterior orbit and near the middorsum of the rostrum, diverging slightly fanwise, and inserting into the mystacial pad.

M. maxillo-naso-labialis (figs. 4, 5) arose from the zygomatic process of the maxilla caudad of the infraorbital foramen. In the Zalophus there was no osteological indication of origin, but in the *Phoca* the

muscle was considerably heavier and the point of origin is marked by a relatively deep fossa, but this is not present in all the Phocidae. Insertion was into the mystacial pad deep to the naso-labialis.

M. mandibulo-auricularis was a complex of several minute and slender muscles which were not separated. Origin was from the dorsal surface of the zygomatic root of the squamosal craniad of the auditory meatus, while insertion, seemingly more intricate in *Zalophus*, was about the auditory tube where this reaches the body surface.

2. MASTICATORY MUSCULATURE

M. masseter (figs. 4, 5, 6) was partially divisible in the *Zalophus* into two portions. The more superficial arose from the cranial third of the zygomatic arch and was inserted along the border of the mandible ventrad of the masseteric fossa, from just rostrad of this to the tip of the angular process. The deeper portion was inseparable craniad from the more superficial, and origin extended caudad as far as the tip of the jugal. Insertion was into the entire masseteric fossa of the mandible ventrad of the base of the coronoid process. In the *Phoca* this muscle was completely divisible, the more superficial arising from the full extent of the jugal, with insertion along the caudo-ventral border of the mandible from just rostrad of the angular process almost to the condyle. The deeper part arose similarly from the rostral end of the jugal caudad to the capsular ligament of the glenoid fossa. Insertion was upon the whole caudo-ventral half or more of the masseteric fossa of the mandible.

M. temporalis (figs. 2, 3, 6) of the *Zalophus* was divisible along its posterior portion into a superficial and a deep part. The former arose by aponeurosis from the medial border of the temporal fossa, rapidly thickened, and was inserted upon the lateral surface of the coronoid process, its more superficial fibers beneath the zygoma blending with the adjoining masseter. The deeper part arose from the entire temporal fossa and inserted upon the medial surface of the whole coronoid process. In the young animal dissected the temporals did not yet approach the middorsal line. In the *Phoca* the temporal was not divisible and was very much weaker and less extensive. Insertion was for a short distance upon the lateral, and upon the entire medial surface of the coronoid process.

M. pterygoideus externus (figs. 4, 5) arose in the *Zalophus* from the bony bridge over the alisphenoid canal, with insertion upon the roughened area directed cranio-mediad upon the medial condyle of the mandible. In the *Phoca* the origin was analogous, from the bridge of bone separating the foramina ovale and rotundum. Insertion was more robust, rostro-ventrad of the condyle upon the medial mandible. Miller found conditions similar in *P. vitulina* and *Arcto-*

cephalus, but the muscle was not mentioned by Murie for *Eumetopias* or *Odobenus*.

M. pterygoideus internus (figs. 3, 4) in the *Zalophus* was much larger than the externus, arising from the border of the bony wall of the interpterygoid fossa and practically coinciding with the extent of the palatal bone along this border. Insertion was below the condyle of the mandible. In the *Phoca* origin was similar save that it extended as far rostrad as the maxillary root of the zygoma. Insertion was along a ridge upon the medial side of the caudal border of the mandibular ramus that extended from the angular process to within a short distance of the condyle. Substantially the same for *P. vitulina* and *Arctocephalus* but not mentioned by Murie for *Eumetopias* and *Odobenus*.

3. INTERRAMAL MUSCULATURE

M. digastricus (figs. 4, 5, 6, 18, 19) was monogastric in both. In the *Zalophus* origin was from the whole lateral border of the paroccipital process, with insertion upon the caudal three-fifths of the ventromedial border of the mandible, extending also just laterad upon a slight prominence ventrad of the masseteric fossa. In the *Phoca* no tendinous division was noted, such as mentioned by Miller for *P. vitulina*, but origin was evidently the same, being from the depression upon the mastoid directly caudad of the center of the bulla. The muscle then spread so as to invest the entire audital bulla. The insertional end was much smaller than in the *Zalophus*, the attachment being to the medial side of the inferior border of the mandible, from the angular process craniad for several centimeters. Murie found a slightly tendinous division of the muscle in *Odobenus*, but not in *Eumetopias*.

M. stylohyoideus (figs. 18, 19) in the *Zalophus* was represented by but a few fibers deep to the digastric, extending from the region of the stylohyal, though not definitely from any part of the temporal bone, with insertion onto the basihyal. In the *Phoca* there was a very thin slip from below the auditory meatus to the basihyal, but superficial to the digastric, as in man. Miller gives this normal origin and insertion for this muscle in his phocids but fails to state its relation to the digastric. In my *Phoca* there was another slip upon the left side deep to the digastric, as in the *Zalophus*, but it seemed to pass entirely dorsad of the basihyal and disappeared in the neighboring tissue. It was noted as questionable in homology and when an attempt was made to verify it upon the right side it could not be found. Murie did not discuss the muscles of this region in his Otariidae.

M. mylohyoideus (figs. 18, 19) was normal for both *Zalophus* and *Phoca.* Origin was from the inner border of the lower jaw, with fibers passing caudo-mediad, and insertion was into the medial raphe and upon the basihyal.

4. MUSCLES OF THE TONGUE

M. mylohyoideus (figs. 18, 19) was normal for both *Zalophus* and arose from the connective tissue about the stylohyal and from a slight prominence upon the audital bulla. (Fig. 4.) It passed closely mediad of the diagastric and thence into the tongue. In the *Phoca* it was similar save that origin was from the inferior lip of the auditory meatus.

M. hyoglossus (figs. 18, 19) arose in the *Zalophus* from the thyro- and basi-hyal, deep to the mylohyoid, passing deep to the styloglossus and extending to the tongue tip. In the *Phoca* it was similar save that the origin was chiefly from the thyrohyal.

M. genioglossus was heavy in the *Zalophus* and arose chiefly from the basi- and cerato-hyals, with relatively few fibers from the lower jaw. Insertion was into the tongue as usual. In the *Phoca* origin was from the lower jaw only, with no direct connection with the hyoid. In this animal there also seemed to be elements of a chondroglossus muscle, represented by fibers passing from the thyrohyal into the tongue. For *P. vitulina* and *Arctocephalus* Miller reported the usual attachments to lower jaw, hyoid and tongue.

MUSCLES OF THE BODY

MUSCLES OF THE NECK

Superficial group.—***M. sternomastoideus*** (figs. 2, 5, 18, 19) in the *Zalophus* arose narrowly from the presternal tip and by fisciculi from its antimere (the juncture being free from the muscles beneath) as far craniad as the thyroid cartilage. Insertion was fascial and along the lateral third of the occipital crest adjoining the cephalohumeral, and more tendinous upon the mastoid process. In the *Phoca* the origin was located more caudad, it being from the border of the presternum, and insertion was limited to the mastoid process. Miller described for *Arctocephalus* a part of the sternomastoid which was utterly unlike anything which I encountered. In addition to the sternal origin, he stated that a part arose from the deltoid ridge of the humerus and from the fascial slip representing the clavicle. The latter part may be homologous with what I am terming the cleidomastoid; but in another place Miller said that it constituted the omohyoid, which, because of its insertion, is hardly

likely. From Murie's text I am unable to judge of the precise degree of resemblance with *Eumetopias* and *Odobenus*.

M. cleidomastoideus (figs. 2, 4, 18) was found in the otariids only. In two it was slender and had origin by fasciculi from the cranial border of the broad or posterior division of the cephalohumeral—this representing the clavicle. Insertion was chiefly tendinous upon the mastoid process adjoining that of the trachelomastoid. No mention of this muscle in *Eumetopias* was made, but Murie found it in *Odobenus*.

Supra- and infra-hyoid group.—**M. omohyoideus** (fig. 18) was fairly well developed in the *Zalophus*. Its origin was inseparable from the deep half of the cleidomastoid, thus arising from the border of the cephalonumeral, this representing the clavicle. It passed beneath the sternomastoid and was inserted upon the basihyal. I do not consider that it was present in the *Phoca*, but Miller says that in *P. vitulina* it was a part of the sterno-thyro-hyoid; and in *Arctocephalus* the outer margin of the sternomastoid, which latter is not to be considered seriously.

M. sternohyoideus et **sternothyroideus.** (Figs. 18, 19.) In the *Zalophus* the former had almost disappeared. There was a single thin muscle arising from the manubrium deep to the presternum with insertion chiefly upon the thyroid cartilage but a separate slip extended also to the hyoid superficial to the thyreohyoid. This was separable from the main muscle no farther caudad than the thyroid cartilage. In the *Phoca* these two muscles were inseparable at their origin from the lateral two thirds of the first costal cartilage. A single thin muscle band then extended rostrad separable into two parts, a superficial slip inserting upon the thyro- and basi-hyals, and a deeper to the thyroid cartilage. Miller said that in *Arctocephalus* the common origin was from the tip of the presternum.

M. thyreohyoideus (figs. 18, 19) was normal, stretching from the thyroid cartilage to the thyrohyal.

M. geniohyoideus (figs. 18, 19) in the *Zalophus* arose from a restricted area near the symphysis menti, and broadened to an insertion upon the entire basihyal. In the *Phoca* this was just reversed, for the origin was broader than the insertion, which latter extended but a few millimeters from the midventral line.

Deep lateral and subvertebral group.—**M. scalenus** (figs. 18, 19). I regard the homology of the different divisions of the scalenus in the pinnipeds as too uncertain to render wise any attempt at present to call them anticus, medius, and posticus, and prefer to refer to them by number. In the *Zalophus* there were two divisions that were almost vestigeal. (*1*) arose from the third rib partly deep to the serratus magnus. It extended as a slender wisp of muscle to a weak

insertion upon the anapophysis of the fourth cervical vertebra. (*2*) was even weaker, extending from the first rib to the anapophysis of the fifth cervical, possibly with a few fibers to the fourth as well. In the *Phoca* there were three divisions. (*1*) arose by digitations from the third to fifth ribs. The one from the fifth arose deep to the most cranical slip of the serratus magnus. There was a dorsal slip superior to the most caudal digitation of the depressor scapulae and another ventral one, both arising from the fourth rib, besides a single ventral slip arising from the third rib. The fibers of all converge to form a tapering, cylindrical muscle which was strongly inserted by tendon upon the anapophysis of the third cervical only. (*2*) arose from the first rib and was inserted upon the anapophyses of the fourth, fifth, and sixth cervical vertebrae. (*3*) also arose

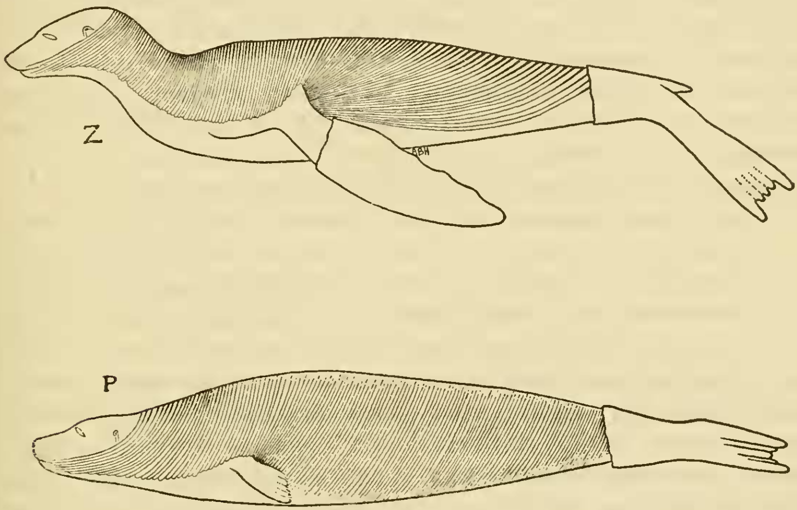

FIG. 15.—LEFT ASPECT OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*) SHOWING PLATYSMA-PANNICULUS CARNOSUS SHEET OF MUSCULATURE

from the first rib but dorsad of the second division. Insertion was by fibrous digitations upon the anapophyses of the third, fourth, fifth, and sixth cervicals. In *Eumetopias* Murie found that insertion of the two divisions was upon the sixth and seventh cervicals; in *Odobenus* that the muscle was single, from the third and fourth ribs to the atlas. Miller gave two divisions for *Arctocephalus* and three for *P. vitulina.* The latter was much as I found it in my specimen, save that insertion was said to be on the parapophyses of the cervical vetebrae. Both origins and insertions of *Arctocephalus* were given as very much more extensive than in my *Zalophus.*

M. longus colli in the *Zalophus* may be said to occur in three portions, but the anterior or atlantic one was exceedingly complex. Its cranial part lay directly laterad of the rectus capitis anterior major

and arose as follows: A ventral slip from the parapophysial plates of the fourth and fifth cervicals. A slip next mediad (separated from the last by a digitation from the posterior oblique division and by the two scaleni) arose from the anapophyses of the fifth and sixth and the parapophysis of the seventh cervical. The third slip arose from the anapophyses of the fourth, fifth, and sixth cervicals. The insertion of the depressor scapulae and slips of the transversalis cervicis then intervened dorsad. A fourth slip arose from the postzygapophyses of the fourth and fifth cervicals and a fifth slip from those of the third and fourth. Between the caudal ends of these two intervened a small part of the biventer cervicis. These five slips then converged to an insertion, largely tendinous, upon the transverse process of the atlas laterad to the inferior oblique. There was no anterior oblique and it is inferred that this division of the longus colli took its place. The second division was as usual, connecting the centra of the cervical as well as an indeterminate number of thoracic vertebrae. The third division or posterior oblique arose within the thoracic cavity from the first few thoracic vertebrae. It inserted by partially tendinous slips upon the parapophysial plates of the fourth, fifth, and sixth cervicals.

In the *Phoca* there were but two divisions. Origins of the first, or rather second, was from a number of the thoracic vertebrae (Miller says seven for *P. vitulina*). It then passed laterad of the rectus capitis anterior major and inserted by four tendinous slips upon the parapophyses of the third, fourth, fifth, and sixth cervicals. Dissection of the more anterior division was unsatisfactory because of caked blood, but origin was evidently from the medial part of the parapophyses of the third to sixth, inclusive, cervical vertebrae. Insertion of each bundle was upon the centrum of the vertebra next rostrad from the fifth cervical at least to the axis and probably to the atlas as well.

There were three parts to this muscle in *Arctocephalus*, and but two were mentioned for *Phoca vitulina*, *Eumetopias*, and *Odobenus*. In all of these the divisions were relatively simple.

M. rectus capitis anterior major (figs. 4, 5) (longus capitis) in the *Zalophus* arose not only from the parapophyses of the third, fourth, and fifth cervicals, but from the centra of the axis and atlas as well. In the *Phoca* it was larger and origin was from the third, fourth, fifth, and sixth cervicals. Insertion in both was upon the mediocranial part of the basioccipital, mediad of the rectus minor. Miller's *Phoca* and *Arctocephalus* dissections agree with my *Phoca*.

M. rectus capitis anterior minor (figs. 4, 5) was very small, arising from the cranial base of the transverse process of the atlas. In both the *Zalophus* and *Phoca* insertion was upon the latero-cranial part

of the basioccipital, laterad of the rectus major. Miller found that in *Arctocephalus* origin was also from the axis.

MUSCLES OF THE TRUNK

Muscles of the thorax.—***M. panniculus carnosus*** (figs. 15, 18) was inseparable from the platysma. In the *Zalophus* the fibers of the latter extended directly ventrad over the scapula, and of the panniculus, converged progressively from the dorsal fascia toward the axilla, clear to the root of the tail. In the extended specimen the ventral border of this muscle passed over the hip, and therefore the knee, with a slight ventral sag, joined the dorsal border of the pectoralis, from which it was separable with difficulty, and inserted into the connective tissue distad of the medial elbow. In the *Phoca* a very different state of affairs obtained. There was no converging of the fibers to the axilla, but origin was somewhat laterad of the middorsal line and all fibers were uniformly directed ventro-craniad at an angle from the vertical of about 35°, covering the knee and extending almost to the base of the tail, in which vicinity the line of origin extended somewhat more dorsad. Insertion of the portion over the scapula was onto the fascia of the middle forearm, and of the remainder upon the fascia of the ventral surface slightly laterad of the midventral line.

Miller found the true panniculus very similar in *P. vitulina* but failed to indicate the degree of convergence of the fibers toward the axilla—a most fundamental point. The platysmal part of this sheet he divided in an unnatural manner, terming the sphincter colli profundus the pectoral panniculus, and the like. Similarly, Murie without a doubt confused his dissection of the panniculus of *Eumetopias*, and not only illustrated the true panniculus as extending in several different directions, due possibly to the "set" position of his specimen, but the parts of the facial musculature which extend over the neck (platysma, spincters colli superficialis and profundus) are shown in incorrect relationship.

M. pectoralis (figs. 9, 10, 18, 19, 20, 22) in the *Zalophus* was imperfectly separable into three parts. The superficial sheet occurred as a pars anticus, arising midventrad from as far craniad as the presternal tip and caudad practically to the fifth costal cartilage; and a pars posticus, arising midventrad from 50 mm. caudad of pars anticus to the xiphoid cartilage. Both of these divisions united and were inserted upon the tough fascia covering the distal palmar aspect of the forearm continuous with the fibrous sheet of tissue immediately beneath the skin of the palm. Muscle fibers ceased about at the wrist. The pars profundus had origin extending from the presternal tip to the xiphoid and converged to a tough aponeurotic insertion along the deltoid ridge of the humerus and the slight ridge extending there-

from to the medial trochlea and thence stretching onto the forearm. (See p. 79.) The part over the deltoid was again divisible at insertion, one fascial sheet extending deep to the other. It should be emphasized that in this genus the border of the panniculus carnosus is practically fused with the border of the pectoralis, forming a powerful sheet of muscle inclosing the trunk, which is of the greatest importance in the economy of the animal. This is very different from the condition in *Phoca*. In this *Phoca* the pectoral sheet was also partially separable into three divisions but in a different manner, and only toward insertion. Origin was from the midvental line from the tough tissue dorsad of the entire presternal cartilage and then ventrad of the whole bony part of the sternal complex. Thence caudad origin passed laterad of the midventral line gradually to the side near the hind limb. From these points the fibers converged to the axillary region. Here it was found that the sheet from the presternum and sternum had become the most superficial, with insertion upon the medial lip of the deltoid ridge, thence by fascia into the axilla, and in the opposite direction, as far as the forearm. There was a second, lateral part, narrow and with the fibers coming from the region of the flanks, and in between these two a third division, the fibers passing deep to the other two and inserting with the second division and with the thicker, ventral part of the latissimus dorsi by a single tough aponeurosis upon the medial lip of the deltoid ridge, just deep to the first division. The sternal part of the pectoral complex was robust, while the abdominal part was thinner.

For *Eumetopias* Murie reported a single superficial pectoral (manubrium to fifth rib) inserting upon the proximal half of the humerus and to the axilla, and a second layer (first rib to xiphoid) with fascial insertion over the arm. In *Odobenus* he found a superficial division from the presternal tip to the xiphoid and ending in the fascia of the forearm, and a deeper, from the fourth costal cartilage to 6 inches caudad of the xiphoid, with insertion upon the whole length of the humeral shaft. In both of Murie's animals there was a narrow third division, not differentiated by me in *Zalophus*, from the manubrium, which merged with the first division. The differences in the pectorals reported by Miller are of a relatively minor nature. Suffice it to say that in this order the pectorals are exceedingly powerful and of great extent.

There is some question regarding the proper treatment in many mammals of the sheet of muscle of which the serratus magnus is a part. In the human the serratus is usually considered as comprising the entire muscle, but reference to the lower Mammalia indicates that it would be wiser to treat it as two muscles. This has at times been done, as by Reighard and Jennings (1901), who term the anterior division the levator scapulae, and I have therefore followed the

same course. This name now seems to me unfortunate, as the levator angulae scapulae is often so called and the two are entirely distinct. It therefore is preferable to refer to it according to its function which is a depressor of the scapula. In various animals this part of the sheet is variable, and purely for convenience it will be divided into a cervical and a thoracic part.

M. depressor scapulae (figs. 7, 18, 19) (levator scapulae part). In the *Zalophus* the cervical part arose by digitations from the anapophyses of the last five cervical vertebrae, directly adjoining the atlantoscapularis superior. It was continuous with the costal part, arising not by distinct slips but practically continuously from the fascia over the angles of the first four ribs. This part passed deep to the costal portion of the scalenus and together with pars cervicis the whole sheet was inserted along the entire vertebral border of the scapula save for about 25 mm. of its most cranial part. The caudal 25 mm. joined the broad tendon of the serratus magnus. In the *Phoca* origin of the cervical portion was the same and of the costal portion, from the ventral terminations of the bony parts of the first two ribs. Insertion was upon the medial aspect of the vertebral border of the scapula from opposite the spine caudo-ventrad around the glenovertebral cartilage. In *Eumetopias* insertion of this, as a part of the serratus magnus, included the atlas, this possibly being my atlantoscapularis superior.

M. serratus magnus (figs. 7, 16, 17, 18, 19) in the *Zalophus* was exceedingly powerful and was placed to best advantage for a backward pull of the scapula. Origin was by fascia from as far craniad as the second rib, thus overlying the depressor scapulae costalis for the distance of two intercostal spaces. Origin continued fascial to the fourth rib and thence to the tenth it was from the bony termination of each rib and the caudal border of its cartilage. The more ventral portion of the muscle was partly aponeurotic but it rapidly increased in thickness until near insertion it was some 10 mm. deep. The more dorsal fibers had an inclination directly craniad to the insertion, 25 mm. in length, upon the glenovertebral angle of the scapula. The anterior half of this was broadly tendinous, and being laterad of a part of the depressor scapulae, fibers of the latter also joined it. In the *Phoca* origin was from as far caudad as the twelfth rib. The digitation from the fifth passed over, and from the third and fourth under, the scalenus. It is doubtful if origin should be considered as reaching farther craniad than the third rib, as anterior to that the muscle sheet was of a much finer texture, but there was no discernible division between this muscle and the depressor scapulae. Insertion was as in *Zalophus*. Miller stated that in *P. vitulina* origin was from as far caudad as the tenth and in

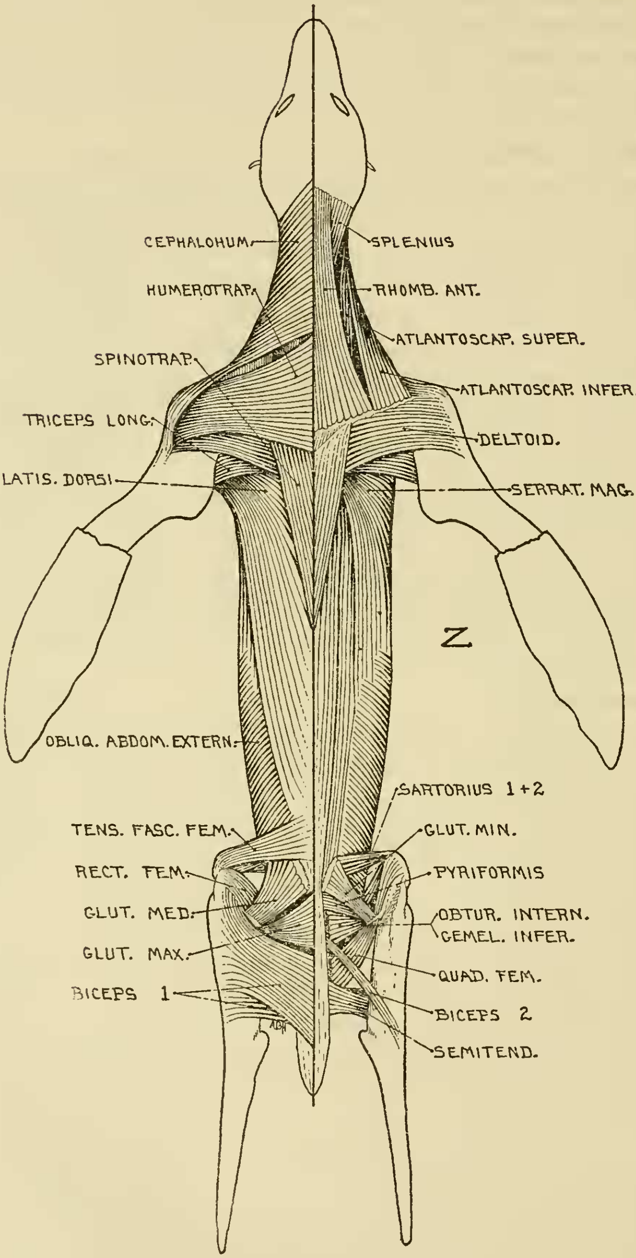

FIG. 16.—DORSAL MUSCULATURE OF ZALOPHUS; SUPERFICIAL LAYER UPON THE LEFT, AND MUCH OF THE NEXT DEEPER LAYER TO THE RIGHT OF THE MEDIAL LINE

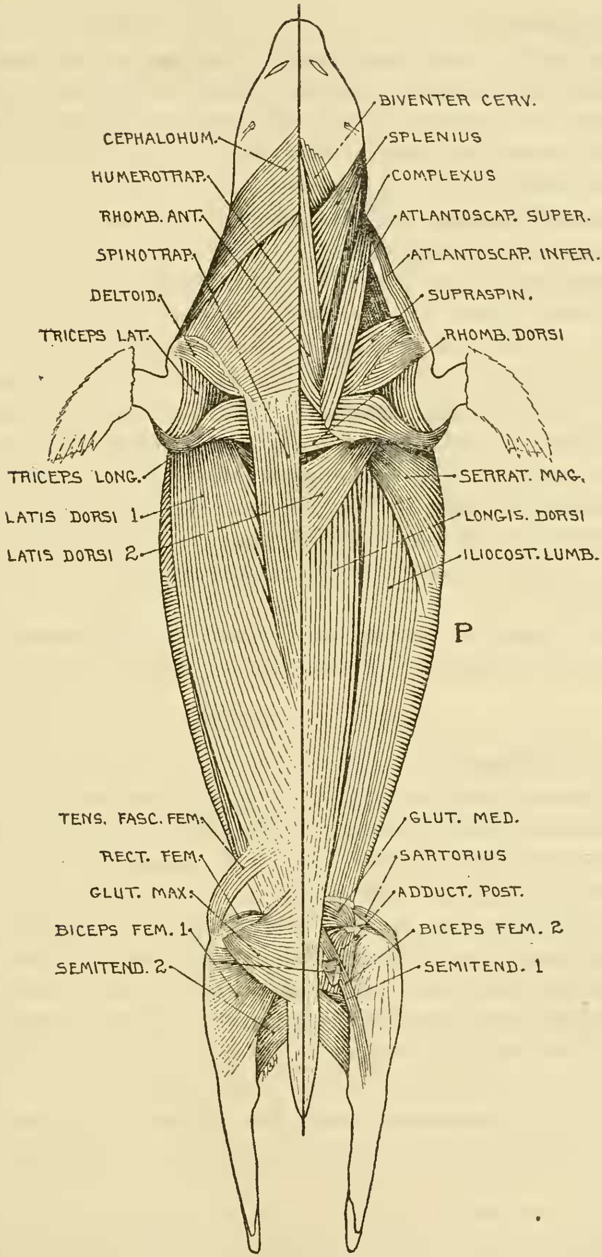

FIG. 17.—DORSAL MUSCULATURE OF PHOCA HISPIDA; SUPERFICIAL LAYER UPON THE LEFT, AND MUCH OF THE NEXT DEEPER LAYER TO THE RIGHT OF THE MEDIAL LINE

Arctocephalus, the eleventh rib. The description for *Odobenus* is obscure.

Mm. intercostales externi (figs. 18, 19) in the *Zalophus* were extensive and covered all the intercostal spaces except a part of these that lay deep to the sternocostalis. In the *Phoca* the external intercostals between the first three ribs did not reach much beyond the bony part of the costae, but caudad therefrom they gradually approached nearer the sternum.

Mm. intercostales interni exhibited no peculiarity save that the lateral fibers almost met over the ribs.

M. sternocostalis (figs. 18, 19) (supracostalis Murie, transversus costarum latus Lucae) in the *Zalophus* arose deep to the pectoral mass from the sternum between the first and fourth costae. Insertion was by two slips passing to the lateral (dorsal) part of the first and second costal cartilages. In the *Phoca* it arose from the manubrium and first two sternebrae, and insertion was upon the first costal cartilage. Miller reported this slightly more extensive in the animals which he dissected, but Murie found it essentially the same as I did. No sternocostalis posterior, such as Miller found in *Phoca vitulina* between the third and seventh ribs, was encountered by me.

Levatores costarum muscles were noted in both genera, but were not followed, nor were any of the muscles within the thorax sought.

MUSCLES OF THE ABDOMEN

M. rectus abdominis (figs. 11, 18, 19) in the *Zalophus* was rather weak. It arose from the symphysis pubis and adjoined the mid-ventral line only as far craniad as the ninth rib. Thereafter slips inserted progressively upon the eighth, seventh, sixth, and fifth ribs, none of these being in contact with the sternum. In the *Phoca* it was relatively much broader and stronger. Discernible muscle fibers disappeared from its medial part at the fifth and from the lateral border at the third rib, from which point a broad tendinous sheet extended with a medial inclination to the sternum as far craniad as the first rib, but not to the presternum. In *Eumetopias* insertion was upon the sixth rib. Minor differences of insertion occurred in the specimens dissected by Miller, save that in *Phoca vitulina* the broad tendon of insertion also extended laterad to the humerus.

Because of excessive contraction of the thorax in the *Zalophus*, the other abdominal muscles were much wrinkled. They were thus very difficult to dissect, and as the preservation of this region in the *Phoca* was poor, all parts, especially craniad, were not completely investigated.

M. obliquus abdominis externus (figs. 16, 19) in the *Zalophus* originated from the last 10 ribs. From the sixth, seventh, and eighth the respective digitations were well marked, but caudad therefrom the slips were distinguishable only with difficulty, they being very tenuous and the fibers precisely parallel with those of the external intercostals. The digitations were not in direct conjunction with those of the serratus, but arose farther dorsad and deep to the latter. Origin was also from the deep dorsal fascia for a short distance. There was no Poupart's ligament, as there was in *Eumetopias* and hence no direct connection with the iliac crest, but a sheet of tough fascia running caudo-ventrad formed a part of the border of the inguinal canal and inserted upon the tuber of the pubis. Insertion was ectad of the rectus almost to the midventral line.

In the *Phoca* this sheet arose from the last 13 ribs, the first few digitations being rather involved in the relationship of their fibers. They were in contact with part of the scalenus, depressor scapulae, and serratus magnus. Caudad of the ribs the fibers of the dorsal border were parallel and in contact with the ilicostalis lumborum or lateral mass of the long system and connected to it by tough fascia. The innominate border developed a Poupart's ligament. Insertion was upon the midventral line ectad of the rectus. In *Arctocephalus* this muscle seems quite similar to *Zalophus* save that insertion is upon the brim of the pelvis, while that of *Phoca vitulina* is essentially similar to my *Phoca*.

M. obliquus abdominis internus in the *Zalophus* arose from the cartilagenous border of the thorax, from the deep dorsal fascia, from the crural arch, extending from caudad of the ventral crest of the ilium to the pectineal process, and then from the border of the pubis to within several centimeters of the symphysis. Insertion was upon the sheath of the rectus. That of the *Phoca* had a similar origin save that the attachment was to Poupart's ligament rather than the brim of the pubis direct. The fibers descended practically no farther ventrad than the border of the rectus, and inserted upon the aponeurotic sheet common to this and the transversalis. In *Eumetopias* the only innominate connection mentioned was with the crest of the ilium.

M. transversalis abdominis in the *Zalophus* arose by interdigitations with the fibers of the diaphragm, ostensibly as usual from the cartilagenous border of the thorax, the deep dorsal fascia, and with the internal oblique from the crural arch. Insertion was upon the deep part of the rectus sheath. In the *Phoca* this muscle did not extend quite to the innominate but the fibers stretched almost to the midventral line.

LUMBAR MUSCLES

M. quadratus lumborum (figs. 11, 24) in the *Zalophus* arose by slender bundles from the last three thoracic and all the lumbar vertebrae. The bundle coming chiefly from the anterior centrum of the penultimate lumbar extended upon the left side of the base of the femoral process of the ilium and its fibers fused with those of the iliacus. Upon the right side this slip of the quadratus inserted fully 2 centimeters farther craniad and was much more slender. In the *Phoca* origin did not extend craniad of the penultimate thoracic vertebra and I could not demonstrate that any of its fibers reached the ilium, but only the sacrum. The whole muscle was very much more robust than in the otariid.

MUSCLES OF THE BACK

Superficial, secondary back muscles.—***M. cephalohumeral*** (figs. 2, 3, 9, 16, 17, 18, 19) should perhaps be placed here. It is formed by the fusion of the clavotrapezius and clavobrachialis as in many carnivores lacking a clavicle. In the *Zalophus* it was rather complex and arose by three heads—a narrow one from the connective tissue just laterad to the tip of the presternum; next a second narrow one from the cranial margin of the deep pectoral, and third a broad head that extended rostrad from the fascia above the entire deltoid ridge of the humerus. The three heads joined and the broad, rather thin sheet of muscle resulting inserted along the medial two-thirds of the occipital crest and thence from the middorsal line as far as the humerotrapezius. Its chief action is probably in certain movements of the head, but in the *Phoca* this was reversed, and it operates rather to move the forearm. In this animal it arose as a tenuous sheet from the middorsal line as far rostrad as the interorbital constriction and caudad beyond the occiput. The fibers passed ventrocaudad over the side of the neck and converged to insert upon the lesser tuberosity and the adjoining portion of the greater as well. Miller stated that in *Arctocephalus* the more caudal attachment was to the humerus only. The condition of this muscle in his *Phoca* was the same as in mine, save that insertion was chiefly upon the greater tuberosity. In *Odobenus* caudal attachment was to the humerus only, but as near as I can tell the condition in *Eumetopias* was more comparable with that of *Zalophus*.

M. humerotrapezius (figs. 3, 7, 9, 16, 17) is homologous with the usual acromiotrapezius. In the *Zalophus* it arose from the middorsum adjoining and in the same plane with the cephalohumeral, the origin extending caudad over a part of the spinotrapezius. The fibers were directed latero-ventrad and it was free from the underlying spine of the scapula along the dorsal two thirds of the latter, but to the ven-

tral third it was intimately attached by fasciculi. Near the insertion its cranial border was overlapped by the cephalohumeral. It inserted, mostly deep to the latter, along the entire deltoid ridge of the humerus and its distal border extended even as far as the forearm, the fibers not ending in fascia but seeming to be incorporated with the supinator longus in company with the deltoid. In the *Phoca* this muscle did not overlie the spine. It arose from the middorsum from mediodorsad of the spine almost to the occiput, this being partially deep to the caudal border of the cephalohumeral. Insertion was robustly along the entire spine of the scapula and also by fascia along the caudal border of the deltoid ridge as far distad as a crater-like fossa, into which inserted a stout tendon which diverged from the humerotrapezius farther dorsad. For *Arctocephalus* Miller's description is not entirely clear, but the muscle seems to resemble that of my *Phoca;* and *Eumetopias* also conforms largely to this pattern—certainly not to that of *Zalophus.* On the other hand conditions in the latter genus were very similar to what Murie encountered in *Odobenus.*

M. spinotrapezius (figs. 7, 16, 17) was long and slender, arising from the middorsum toward the caudal thorax. In the case of the *Zalophus* there was a deep, tough aponeurosis upon which most of the fibers inserted, but more ectad there was a flat tendon developed and this ran cranio-ventrad to the spine near the ventral border of the muscle. That of the *Phoca* was similar save that the muscle fibers inserted directly upon the spine. In *Arctocephlus* insertion is said to be by the fibers blending with the dorsal surface of the deltoid.

M. latissimus dorsi (figs. 9, 16, 17) in the *Zalophus* arose from the dorsal fascia, extending from a few centimeters craniad of the glenovertebral angle of the scapula to the vicinity of the last rib. The anterior border passed superficial to the glenovertebral angle and the fibers of the whole sheet converged to two partially separable insertions—the more dorso-cranial one, representing perhaps two-thirds of the muscle, to a fascial insertion along the border of the teres major, and the other, to a fleshy insertion along the dorsal border of the insertional end of the pectoralis. For *Eumetopias* this muscle was reported as single, with insertion upon the bicipital ridge. Its insertion was not given for *Odobenus.* In the *Phoca* the dorso-cranial part was quite thin, with origin gradually from the dorsal fascia and fibers converging to the axillary tissue. The ventral part was rather abruptly 10 times as thick as the remainder, with insertion upon the deltoid ridge with the second and third divisions of the pectoralis.

M. rhomboideus anticus (figs. 2, 3, 7, 16, 17) in the *Zalophus* arose from the medial third of the occipital crest deep to the cephalo-

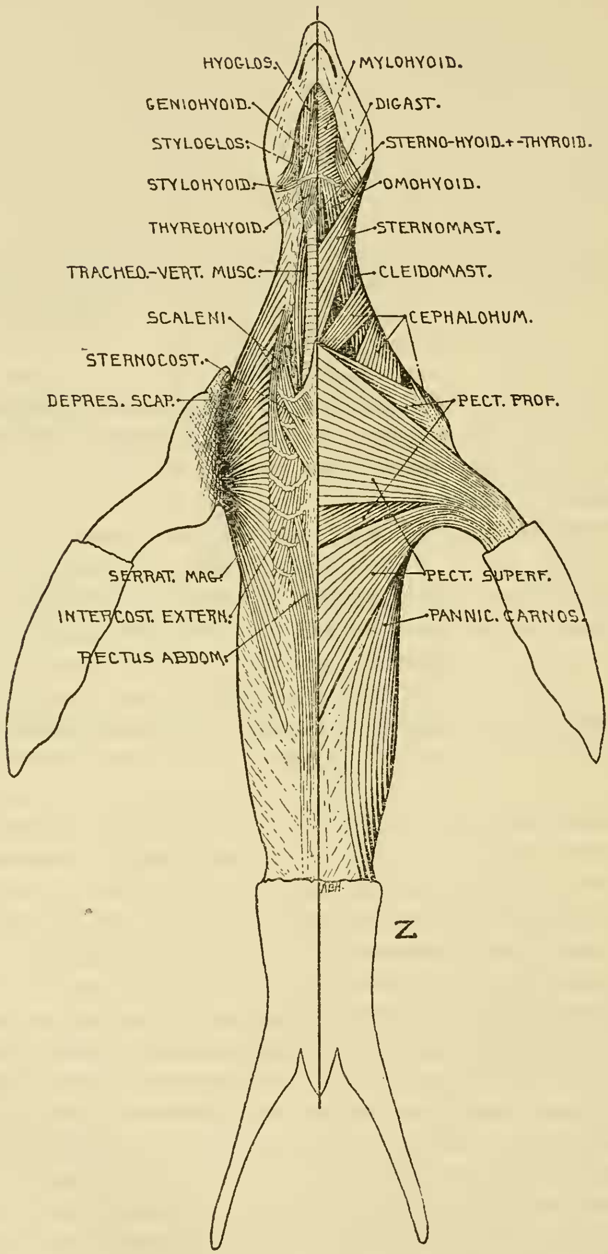

FIG. 18.—VENTRAL MUSCULATURE OF ZALOPHUS; SUPERFICIAL LAYER UPON THE RIGHT, AND MUCH OF THE NEXT DEEPER LAYER TO THE LEFT OF THE MEDIAL LINE

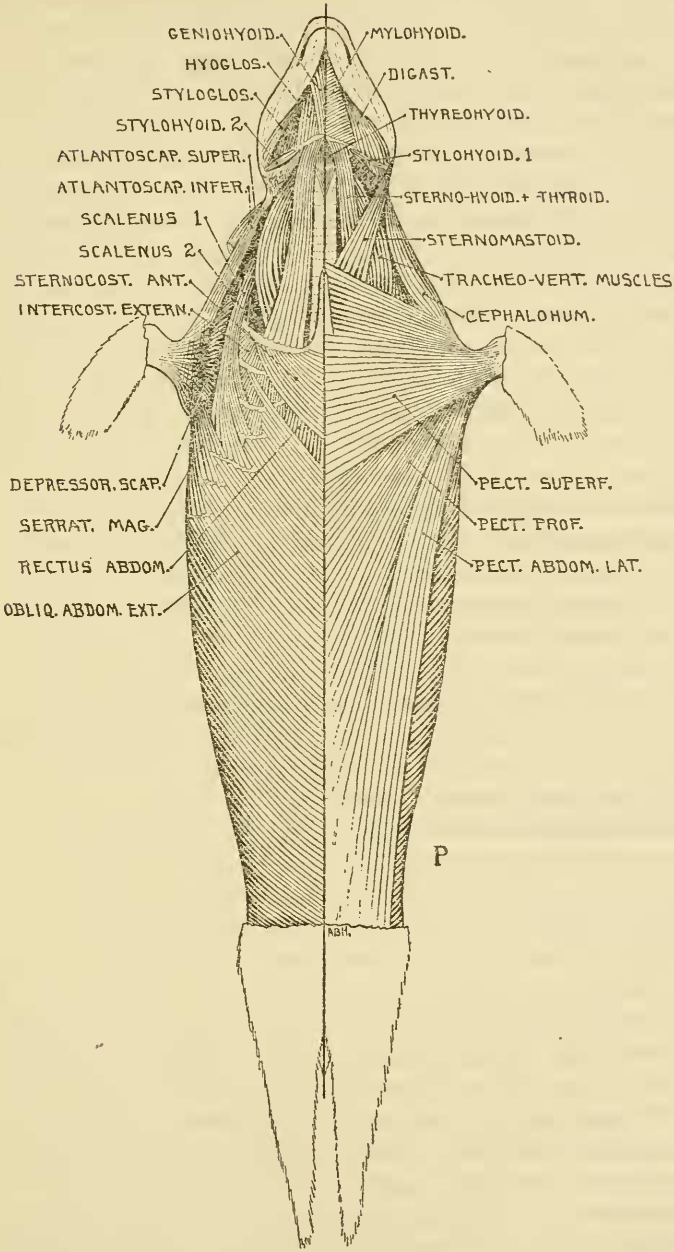

FIG. 19.—VENTRAL MUSCULATURE OF PHOCA HISPIDA; SUPERFICIAL LAYER UPON THE RIGHT, AND MUCH OF THE NEXT DEEPER LAYER TO THE LEFT OF THE MEDIAL LINE

humeral and inserted along the dorsal three-fifths of the spine of the scapula. In *Arctocephalus* this was called rhomboideus capitis by Miller and was similar to my *Zalophus*. According to Murie conditions were quite different in *Eumetopias*. He termed it rhomboideus capitis, with origin from the middorsum of the cervical and anterior thoracic region and insertion upon the dorsal part of the spine and the caudal half of the vertebral border of the scapula. In *Odobenus* it did not extend caudad of the spine along the vertebral border. In my *Phoca* origin was from the nuchal ligament as far craniad as the occiput. It passed deep to the vertebral border of the scapula and inserted along the caudal border of the glenovertebral cartilage, its fibers fasciculating with those of the serratus magnus. For his *Phoca* Miller described two anterior rhomboids—a capitis and a cervicis—but from his text I can not tell whether these were entirely separate muscles (one corresponding to an occipitoscapularis) or two divisions of what might be considered as a single sheet. Attachment to the whole vertebral angle of the scapula is indicated, but otherwise conditions were similar to my *Phoca*.

M. rhomboideus dorsi (figs. 7, 17) in the *Zalophus* arose from middorsad by interdigitations of its fibers with those of its antimere. It was a rather decadent muscle, and its coarse, loosely connected fibers ran laterad to insert upon the vertebral border of the scapula, from slightly craniad of the spine to the glenovertebral angle. Murie considered that this represents the major and minor divisions. In the *Phoca* it was similar, save that insertion was only by fasciculi into a part of the insertion of the serratus magnus along the ventral border of the glenovertebral cartilage.

M. atlantoscapularis superior (figs. 7, 16, 17, 19) in the *Zalophus* had origin from the transverse proceess of the atlas just entad of the inferior division of this muscle. It was slender and extended to aponeurotic insertion upon the vertebral border of the scapula for a short distance just craniad of the spine. Near the insertional end it was parallel to the fibers of the depressor scapulae and one can readily see that the two muscles might fuse, the sheet then being folded over the coracovertebral angle. Authors have expressed doubt, from time to time, that either division of this muscle as here termed is homologous with the human levator (anguli) scapulae. The innervation in a large number of diverse mammals will have to be investigated before this point is settled, but at any rate it would be theoretically easy for this superior slip to migrate ventrad along the anterior border of the scapula, or for the inferior slip to migrate on to the head of the humerus, as is actually the condition in *Phoca*, and then dorsad to the more usual levator anguli scapulae position. Conditions were the same in my *Phoca* save that insertion was dor-

sad of the spine. Not mentioned by Murie as a distinct muscle in *Eumetopias* but possibly included as a part of his serratus magnus.

M. atlantoscapularis inferior (figs. 7, 9, 16, 17, 19) also arises from the transverse process of the atlas, but superficial to the origin of the superior division. In the *Zalophus* insertion was by fascia upon the ventral two-fifths of the spine of the scapula adjacent to the anterior rhomboid and upon the neighboring part of the humerus. In the *Phoca* the insertion had migrated more distad and was by fascia upon the greater tuberosity and deltoid ridge of the humerus adjoining (ventrad of) the humerotrapezius. Miller called this muscle atlantohumeral in *Phoca* and atlantoscapular in *Arctocephalus*, according to the insertion. They are undoubtedly homologous and I prefer to employ the same term for both, even though it is slightly ambiguous in the case of the seal. It is the levator anguli scapulae of Murie. In addition the latter mentions, rather vaguely, an accessory slip in *Odobenus* which he considers to be the homologue of a levator claviculae.

M. serratus posticus. Deep to the rhomboid layer of the *Zalophus* and a couple of centimeters caudad to any part of the scapula was a tenuous, vestigeal bit of muscle which arose from fascia and ended likewise beneath the caudal border of the larger rhomboid. I did not distinguish it in my *Phoca*, possibly because of the presence of clotted blood in this region, but Miller did in his. It has not been reported from any of the other eared seals proper, but Murie found it fairly well developed in *Odobenus*.

Deep, intrinsic back muscles.—***M. splenius*** (figs. 2, 5, 16, 17) arose from the middorsum, extending in the *Zalophus* from the occiput to about the second thoracic spine, and inserting along the entire occipital crest, from the vertex to the mastoid process, at the latter point being continuous with the trachelomastoid. In the *Phoca* origin extended craniad only as far as the spine of the axis, and insertion was limited to the mastoid process. This is Murie's splenius capitis.

M. erector spinae, sacrospinalis, extensor dorsi communis or long system of the back was but moderately developed in the *Zalophus*, and the pair of muscles together in the specimen dissected measured but 100 mm. in width at the widest part in the posterior thoracic region. It was indivisible in the lumbar region, the whole muscle arising from the vertebrae, sacrum, and inner surface of the ilium. Between the ninth and sixth ribs it was partly separable into an iliocostalis dorsi and longissimus portion, but craniad to the sixth rib these once more to all intents constitute a single muscle. This fused part sent a slip to each of the first 10 ribs and to the anapophyses of each of the last five cervical vertebrae, this part at least

representing a longissimus cervicis. Mediad, and craniad of the fourth thoracic vertebra, the biventer cervicis intervened, and adjoining the spines was the spinalis dorsi, distinguishable with clarity craniad of the eighth rib. The spinalis cervicis portion of this inserted upon the cervical spines to and including the axis.

In the *Phoca* this was an astonishing mass of muscle, the two sides together measuring 210 mm. in width, and a definite impression was gained that although enormously stronger than in the eared seal dissected, its normal uses were for less complicated and more restricted in movements. Caudad it was clearly divisible into a medial longissimus dorsi and an iliocostalis lumborum of slightly lesser width. These two, however, were not separable with any degree of east throughout their deeper portions. The superficial fibers of the iliocostal part were seen to arise from the glistening aponeurosis covering the longissimus, but the chief origin was fleshy and from almost the entire cranially-directed surface of the "medial" border of the ilium, forming an attachment of enormous strength. Within 50 mm. of this bone the iliocostal had attained a width of 40 and a depth of 45 mm. More craniad there was fibrous connection with the ribs over which it passed until a tendinous slip was given off to join the seventh, but apparently no other ribs in that vicinity. The muscle then broadened and developed tendon bundles, five of these passing cranio-dorsad to join the transverse processes of the first five thocacic vertebrae and four others cranio-ventrad to join the first four ribs. Thus, the anterior part of this muscle was simple, doing little but acting as an anchor for the posterior part. In the posterior thoracic region the longissimus had rather obscure spinalis dorsi elements, there being tendons extending cranio-mediad to join each spine, but no distinct muscle could be separated. In its more lateral part the longissimus had slight fibrous attachment to the ribs and mediad there were tendons gradually developing from the transverse processes extending craniad to be lost in the muscle mass. These increased in size in cranial sequence from the last thoracic and the series culminated in a very strong tendon from the tenth after which these ceased. Thus, these tendons seemed to be largely instrumental in the development, upon these thoracic vertebrae only, of distinct metapophyses and constituted a semispinalis dorsi element. There were also smaller longissimus tendons of opposite inclination attached to the anapophysis of each vertebra. At about the seventh thoracic the longissimus split into two parts, both rapidly becoming slender. The more medial was the spinalis dorsi, becoming the spinalis cervicis. Its attachments were by fasciculi to the spines as far as the fourth cervical, although a few fibers may have extended still farther craniad. The more lateral division was the longissimus

(transversalis) cervicis. It sent tendinous slips to the transverse processes of the first four thoracics and was tucked in laterad of the trachelomastoid, inserting upon the dorsal part of the anapophyses of the last four cervicals.

M. trachelomastoideus[4] (figs. 2, 5), or longissimus capitis, although a part of the long system morphologically, had better be considered a separate muscle. In the *Zalophus* it arose from the postzygapophyses of the last four cervical and first two thoracic vertebrae, and insertion was strongly upon the mastoid process continuous with that of the splenius. In the *Phoca* origin was from the third to seventh (inclusive) cervicals. Miller reported that in his *Phoca* the muscle was partially divisible, a second slip inserting upon the transverse process of the axis; but nothing like this occurred in my specimen. In *Arctocephalus* origin was from the last five cervicals only; in *Eumetopias* from the fourth and fifth and in *Odobenus*, the fifth and sixth thoracic spines, according to Murie, who terms this the splenius colli.

M. biventer cervicis (figs. 2, 17) in the *Zalophus* had origin by partly tendinous slips from the postzygapophyses (or their vicinity) of the first four thoracic and last two cervical vertebrae. Insertion was upon the middorsal line for several centimeters caudad of the vertex, and for about two centimeters along the medial occipital border. In *Arctocephalus* origin is said to be from the second, third, and fourth thoracic vertebrae: In *Odobenus* "from the seventh dorsal"; in *Eumetopias* "from the fifth, second, and first dorsal spines."

M. complexus (figs. 2, 17) in the *Zalophus* arose by slips from the vicinity of the postzygapophyses of the middle five corvicals, the one to the sixth lying mediad of the cranial border of the biventer cervicis. Insertion was rather narrow in a tendinous sheet for a couple of centimeters along the occipital border laterad to the insertion of the biventer cervicis. In *Arctocephalus* and *Eumetopias* origin is said to be from the third to seventh cervicals; in *Odobenus* "from the fifth anterior dorsal."

In my *Phoca* the biventer cervicis and complexus were indivisible, forming the following:

M. semispinalis capitis (fig. 3), arising in this *Phoca* from the vicinity of the postzygapophyses of the last six cervical and first two thoracic vertebrae. It was a heavy muscle at origin, the fibers converging to a thin, aponeurotic insertion upon the medial third of the occipital crest. Miller, however, apparently had no trouble in separating this muscle in his *Phoca vitulina* into a biventer and complexus, but the attachments were very similar to those of mine.

---

[4] It is believed that in the case of the wood rat (Howell, 1926) the two divisions of the biventer cervicis as stated should rather have been considered to comprise both that muscle and the complexus, while the complexus, so termed, is in reality the tracehlomastoid.

M. rectus capitis posterior major (figs. 2, 3) in the *Zalophus* arose not only from the whole length of the spine of the axis but also from the periosteum over the spine of the third cervical. Insertion was upon the supraoccipital laterad to the border of the biventer cervicis. In the *Phoca* it was larger and covered both the minor division and the inferior oblique as well. Origin was from practically the entire length of the axial spine and insertion was upon the occiput from the vertex almost to the lateral margin of the semispinalis capitis insertion. In *Arctocephalus* and *Eumetopias* origin was confined to the axis. In *Odobenus* it also "has attachments to the five posterior cervical zygapophyses."

M. rectus capitis posterior major acessorius (fig. 3), so termed by Miller and Murie for the animals which they dissected was not distinguished in the *Zalophus*, but in the *Phoca* arose from the cranial border of the axial spine, with insertion upon the occipital between the superior oblique and minor rectus.

M. rectus capitis posterior minor (figs. 2, 3) lay deep to the last. It took origin from the dorsal arch of the atlas and inserted upon the supraoccipital deep to the last. In the *Phoca* it was similar save that the insertion was situated mediad to the accessory part of the major division.

M. obliquus capitis superior (figs. 2, 3) arose from the transverse process of the atlas, with insertion strongly upon the lateral part of the occipital plane.

M. obliquus inferior in the *Zalophus* arose from the spine of the axis deep to the rectus major, with insertion upon the transverse process of the atlas. In the *Phoca* it seemed to be easily divisible into two similar parts. Miller found it single in his *Phoca*, however.

The perineal muscles were not investigated but it was noted that the levator ani, apparently occurring in two divisions, was poorly developed, or rather that the fibers were coarse and separated by much fatty tissue.

MUSCLES OF THE ANTERIOR LIMB

MUSCLES OF THE SHOULDER GIRDLE

M. supraspinatus (figs. 7, 9, 16, 19, 20, 21) was complex in the *Zalophus*, as is often the case. Origin was from the entire supraspinous fossa and anterior surface of the spine. Near the insertion it was separable into two slips, the more dorsal inserting upon the tip of the greater tuberosity with a few fibers passing also to the lesser. The second slip inserted upon the greater tuberosity also, just distad of the tip. In the *Phoca* origin was the same, and the muscle was partially divisible ectad, as indicated in Figure 21. Insertion was upon the greater tuberosity and upon the ligament extending from

the greater to the lesser. In the animals dissected by Murie and Miller this muscle was essentially the same, with minor variations.

M. infraspinatus (figs. 7, 9, 20, 21) in the *Zalophus* probably had not more than one-fifth the strength of the supraspinatus. It arose over the spinal two-thirds of the infraspinous space and converged to a slip that passed over the lateral head of the femur to insert upon a slight ridge upon the lateral base of the greater tuberosity. In the *Phoca* this muscle was even much smaller—to a surprising extent. Origin was from the deep part of the spine and about one-half of the narrow space which constituted the infraspinous part of the scapula. It passed craniad over the acromial notch and inserted upon the capsule of the shoulder joint adjoining the supraspinatus and over the greater tuberosity.

The ventral part of the cephalohumeral is homologous with a part of the deltoid. The only remaining part of the latter was the deltoid.

M. deltoideus (figs. 7, 9, 17, 20, 21). In both my specimens this was relatively very powerful and overlay almost all of the infraspinous part of the scapula. In the *Zalophus* it arose by tendinous and fleshy fibers from the entire posterior border of the spine of the scapula and by tough aponeurosis from the dorsal border of the infraspinous fossa, although muscle fibers were not found so far dorsad near the spine. Insertion was aponeurotic, chiefly along the lateral border of the deltoid ridge, but a tendinous slip also passed to the ectepicondyle of the humerus, and the distal border passed inseparably into the substance of the supinator longus. In the *Phoca* origin was only from the caudal border of the spine, with insertion partly tendinous upon the caudal border of the deltoid crest. In *Arctocephalus* no mention was made of any junction with the supinator longus, but it was stated that a "tendinous slip goes to the fibro-cellular bar lying upon the anterior border of the radius." In *Odobenus* there was no connection with the supinator longus.

M. teres minor (fig. 7) in the *Zalophus* was exceedingly thin but broad at origin, which was from the "teres major fossa," or the posterior third of the infraspinous space. It apparently fused with the subscapularis over the axillary border and the insertion was inseparable. In the *Phoca* it was as broad distad as, but much thinner than, the infraspinatus. It arose not as in *Zalophus* but aponeurotically from the distal half of the ridge between the two concavities of the infraspinous space, and was located between the latter muscle and the triceps. Near insertion the fibers joined the tendinous deep belly of the deltoid, and were inseparable. Miller stated that in *Phoca vitulina* insertion was upon the greater tuberosity and the capsule of the joint; but he did not find it in *Arctocephalus*. In *Eumetopias*

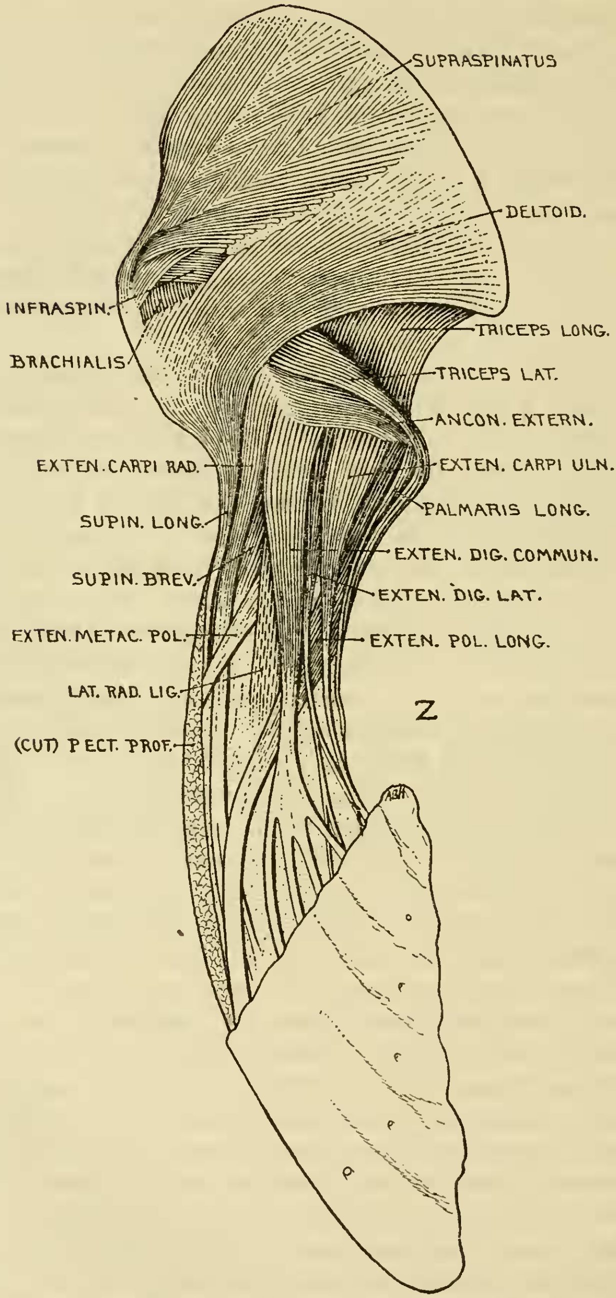

FIG. 20.—SUPERFICIAL MUSCULATURE OF THE LATERAL ASPECT OF THE LEFT ANTERIOR LIMB OF ZALOPHUS

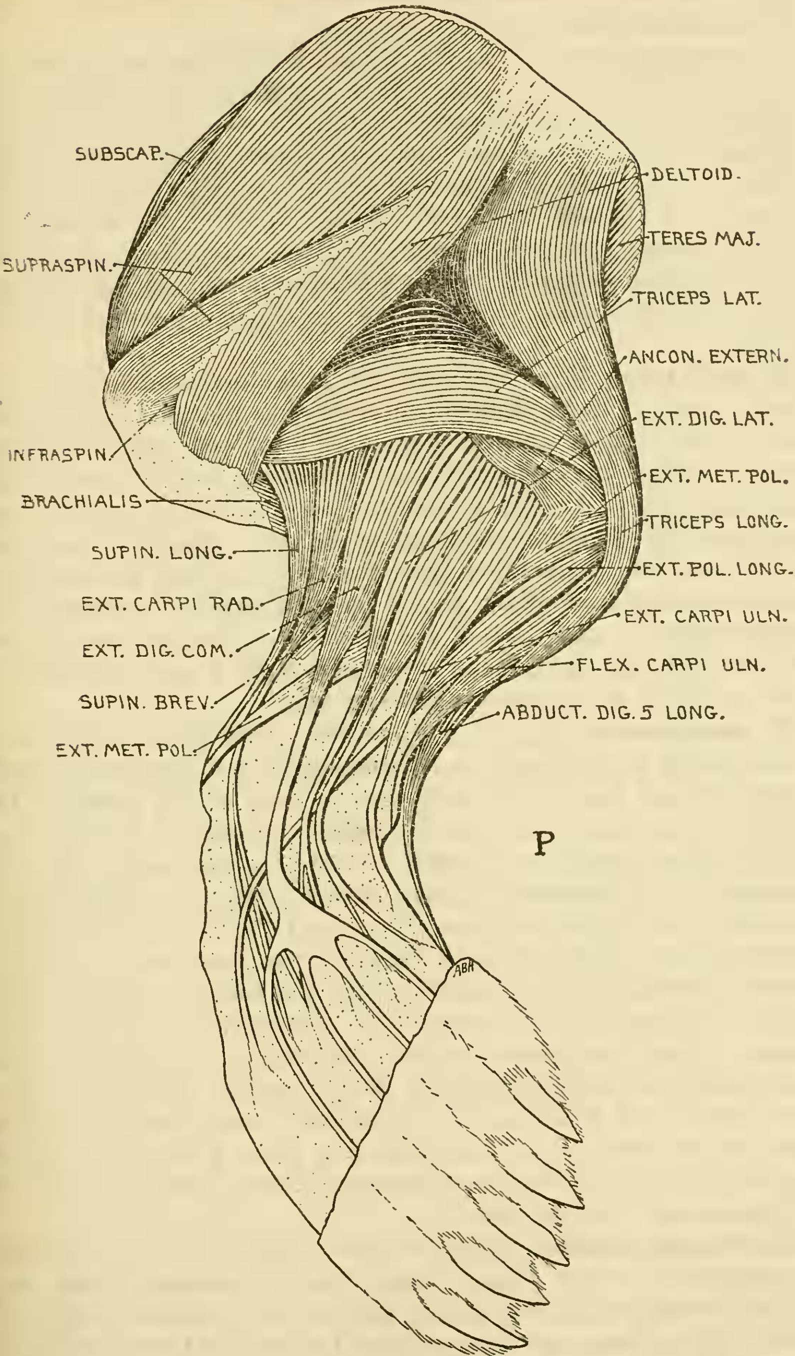

FIG. 21.—SUPERFICIAL MUSCULATURE OF THE LATERAL ASPECT OF THE LEFT ANTERIOR LIMB OF PHOCA HISPIDA

Murie reported it in close union with the teres major, and in *Odobenus* he did not succeed in segregating it.

M. teres major (figs. 7, 9, 21, 22, 23) in the *Zalophus* arose from the more dorsal part of the axillary border of the subscapularis and by fasciculi from the dorsal quarter or third of the axillary border of the bone. The insertion was broadly tendinous at about the middle of the humeral shaft and under cover of the biceps. In the *Phoca* it arose over practically the entire axillary half of the infraspinous space, including the glenovertebral cartilage. It passed between the triceps and the subscapularis to insert upon the well-defined rugosity in the bicipital groove of the humerus, slightly proximad to the middle.

M. subscapularis (figs. 9, 21, 22, 23) exhibited complexity of its fibers, as usual. In the *Zalophus* it arose from the entire medial surface of the scapula and even extended over the axillary border, while insertion was upon the lesser tuberosity deep to that of the episubscapularis. In the *Phoca* it was exceedingly massive, and overhung both the cranial and axillary borders. The latter part was partly separable, originating from the ventral border of the glenovertebral angle, and might almost be considered as constituting a separate muscle. Insertion of the whole was upon the lesser tuberosity, in this case larger and more prominent than the greater, a fact due chiefly to the power of this muscle.

M. episubscapularis (figs. 7, 22), in the nomenclature of which I follow Miller for convenience, is undoubtedly a division of the subscapularis and was folded over upon a part of the latter in the *Zalophus* only. It arose from the medial coracovertebral angle and border of the scapula and passed over the cranial edge of the subscapularis. It developed a tough tendon within the substance of the muscle which branched, one slip going to the lesser tuberosity in company with muscle fibers. The other was attached to a faintly defined groove upon the medial part of the ridge extending distad from this tuberosity and beneath the insertional end of the teres major. Upon this tendon and the adjoining dorsal border of the teres major the remaining muscle fibers inserted. This muscle has been found in all of the eared seals so far dissected, and the walrus also. Murie seems to have considered it to be a derivative of the supraspinatus in his report on *Eumetopias*, but listed it as a part of the subscapular for *Odobenus*.

M. subscapulo-capsularis (fig. 9) is found in the *Phoca* only, and was represented by a few fibers arising from the extreme distal part of the subscapular surface of the scapula, with insertion upon the capsule of the joint and the adjoining base of the lesser tuberosity. Miller stated that in *Phoca vitulina* it arose from the base of the axillary border.

MUSCLES OF THE UPPER ARM

The flexors comprise two single muscles:

M. biceps brachii (figs. 7, 10, 22, 23) was single and took origin, largely by tendon, from the rudimentary coracoid process upon the cranial margin of the glenoid cavity. In both genera it passed through the bicipital groove, between the greater and lesser tuberosities and was inserted by tendon onto the bicipital rugosity of the radius.

M. brachialis (figs. 9, 10, 20, 21, 22) was also single, with origin in the *Zalophus* from the cranial half of the proximo-lateral shaft of the humerus and from the caudo-lateral border of the deltoid ridge. A few of its fibers fused with the supinator longus. In the *Phoca* origin was from practically the whole of the lateral shaft of the humerus caudad of the deltoid ridge. In both animals the muscle passed deep between the supinator longus and pronator teres to insert by a strong tendon upon the rugosity just distad of the lesser sigmoid cavity of the ulna. Murie and Miller wrote that in *Eumetopias* and *Arctocephalus* this muscle arose by two heads, the two together being very similar to the one in my *Zalophus.*

Murie reported a very weak coraco-brachialis in *Odobenus*, but I am not at all convinced by his text that he was not mistaken in this.

In contrast to the paucity of flexors, the extensors of the brachium are powerful and specialized.

M. epitrochlearis (fig. 22) (as of Reighard and Jennings, not the dorsoepitrochlear of some authors) was found in the *Zalophus* only, but neither Murie nor Miller seem to have encountered a similar muscle during their dissections of eared seals, they, perhaps, having considered it as integral with the triceps. It has, however, all the characteristics of a normal epitrochlear as found in so many mammals, save that the great specialization of the long triceps has caused the latter to curve around partly superficial to it. It arose from the fascia and connective tissue investing the medial part of the triceps longus and latissimus dorsi. The fibers ceased in the fascia of the ulnar border of the forearm, and thus the insertion had migrated somewhat distad, as have so many other muscles of the anterior extremity.

The true triceps had best be considered as consisting of three parts as usual.

M. triceps longus (figs. 7, 10, 16, 17, 20, 21, 22, 23) in the *Zalophus* was divisible into two portions. The more caudal part arose from the dorsal third of the slight ridge that bisects (roughly) the infraspinous space of the scapula, and by an aponeurosis covering the teres major. It passed to the olecranon, twisted in a peculiar manner, and was attached rather lightly at this point. It was then ap-

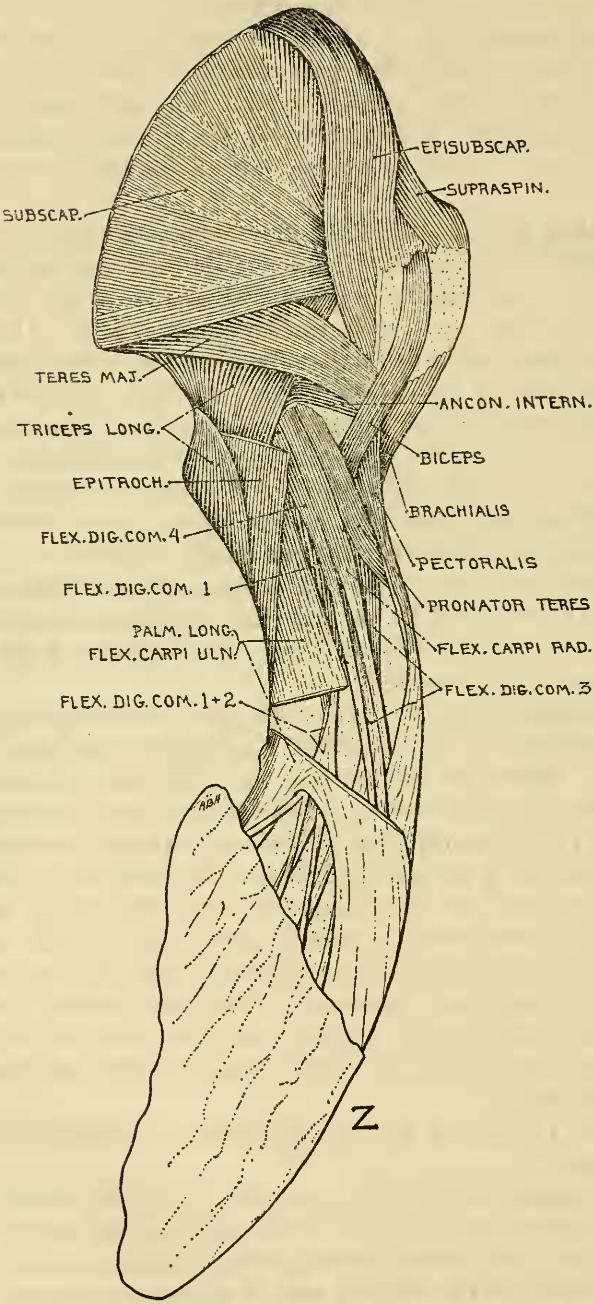

Fig. 22.—Superficial musculature of the medial aspect of the left anterior limb of Zalophus

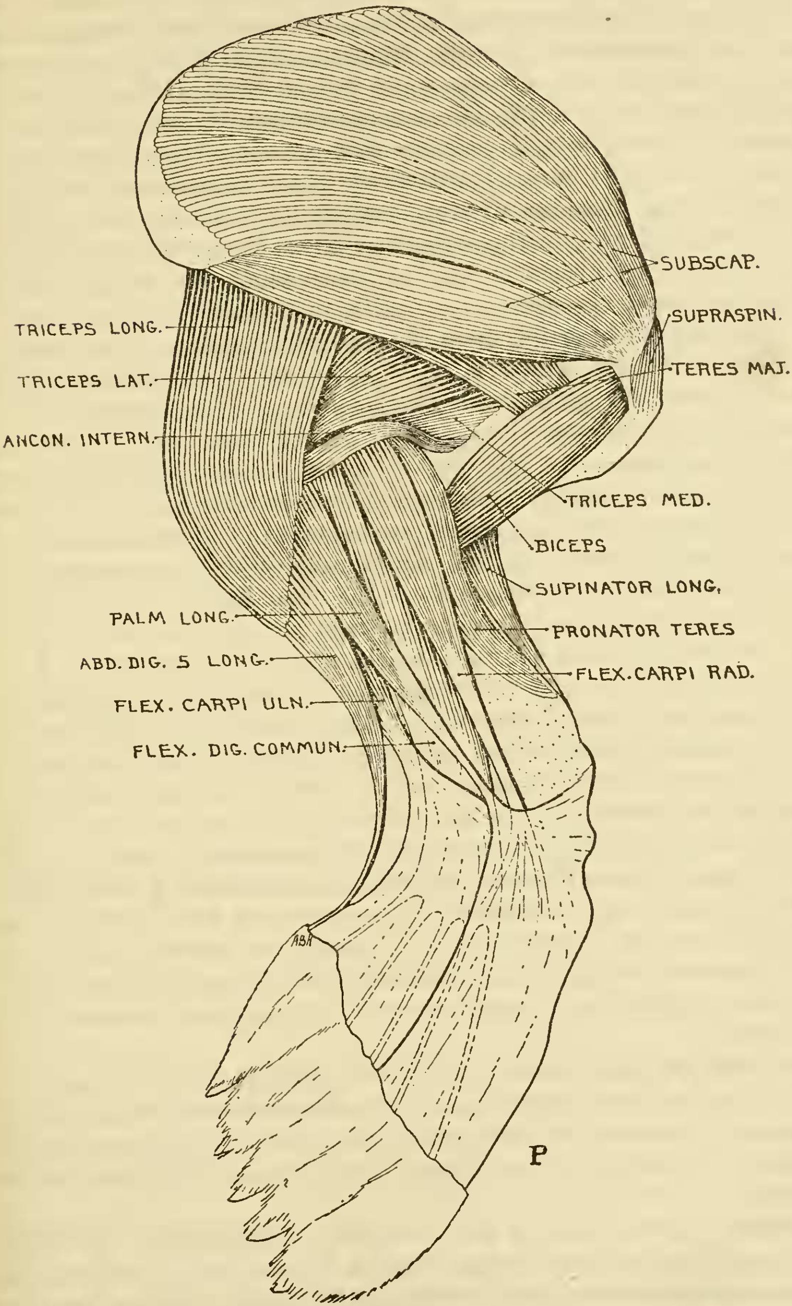

FIG. 23.—SUPERFICIAL MUSCULATURE OF THE MEDIAL ASPECT OF THE LEFT ANTERIOR LIMB OF PHOCA HISPIDA

parently inseparable from the adjoining part of the lateral triceps. It disappeared in fascia over the ulnar border of the forearm. The more cranial division did not really constitute a distinct muscle but was easily separable. It arose from the distal half of the central ridge of the infraspinous space and was strongly inserted upon the medial olecranon and (by fascia) onto the medial epicondyle of the femur. In the *Phoca* I consider this muscle to have been single. It arose from the dorsal third of the ridge upon the infraspinous space and thence the line of origin curved about the adjoining part of the vertebral border of the scapula as far as the spine, in contrast to this part of the origin in the *Zalophus* which was directed *away* from the spine. It became very thick and passed over the elbow to a rather abrupt insertion upon the superficial fascia of the forearm.

M. triceps lateralis (figs. 7, 9, 10, 17, 20, 21, 23) in the *Zalophus* arose partly from the aponeurosis covering the cranial portion of the long head, but chiefly by narrow fasciculi from the latero-caudal neck of the humerus. The borders of this muscle were distinct but the deep fibers blended with those of the medial head. With the latter there was also some fibrous attachment to the olecranon but the muscle finally passed over this and together with the adjoining part of the long head was directed down the ulnar border of the forearm and disappeared in fascia above the wrist (in fig. 20 the edge of this part of the muscle is shown trimmed away). In the *Phoca* I list this muscle as occurring in two divisions. The more lateral and the one shown in figure 21 arose from an area that really constitutes the latero-caudo-proximal border of the deltoid ridge, quite to the head of the humerus. There is considerable question in my mind as to whether the second division does not really belong with the triceps longus—a point difficult to prove by the innervation. But the origin was separated from that of the true long triceps by a considerable interval and it seems more natural to place it with the lateral division. It arose from the distal (cranial) third of the central ridge of the infraspinous space, passed down the back of the brachium and joined the first division, both inserting upon the more dorsal process of the olecranon.

M. triceps medialis (figs. 9, 10, 23) arose from the entire caudal part of the shaft of the humerus and was continuous with the anconeus externus. Insertion in both genera was upon the expanded radial aspect of the olecranon, and slightly from the caudal or dorsal aspect as well.

Miller reported that in his *Phoca* and *Arctocephalus* conditions were on the whole very similar to what I found in my seal and sea lion, respectively, save that he divided the triceps into four parts—a dorsi-epitrochlear corresponding to my first division of the long head in *Zalophus* and long head in *Phoca*. In his *Phoca* origin was from

the dorsal border of the scapula only. His long head corresponds to the lower division of the long head in *Zalophus* and upper division of the lateral head in my *Phoca*. His external head corresponds to my lateral head in *Zalophus* and lower division of the lateral head in *Phoca*. And his internal head corresponds to my medial one. Murie listed four similar divisions for *Eumetopias* and *Odobenus*. Humphry reported that in *Phoca* the long head reached the paddle, which has not been confirmed by anyone since.

M. anconeus externus (figs. 9, 10, 20, 21). It is only because Murie and Miller listed this as a muscle separate from the medial triceps that I follow the same course, for in both my specimens the two were fused. In both genera it may be said to originate from the lateral epicondyloid ridge, with insertion along the dorsal two-thirds of the external border of the olecranon.

M. anconeus internus (figs. 9, 10, 22, 23) has origin from the same situation in both *Zalophus* and *Phoca*—the entepicondylar ridge—save that in the former it was from the most prominent part of the bone, and in the latter, caudad of the entepicondylar foramen, rather than from the more prominent part craniad thereto. Insertion of both was upon the tuberosity upon the medio-dorsal part of the olecranon.

MUSCLES OF THE FOREARM

The flexors consist of the following muscles:

M. palmaris longus (figs. 10, 20, 22, 23) was of phenomenal power in the *Zalophus* and was fused with the flexor carpi ulnaris. The two together arose from the entire medial surface of the broad proximal half of the ulna, including the olecranon. Certain of the more superficial fibers decussated with those of the border of the triceps longus. It rapidly became broadly tendinous (25 mm. wide) as it passed over the wrist, was attached (the flexor ulnaris portion) to the pisiform, and then spread as in Figure 22, a powerful branch going to digit 1, and a weaker to digit 5, deep to its flexor sublimis tendon. It is perhaps the strongest flexor of the manus, working upon the two borders in an extraordinarily powerful cupping action. In the *Phoca* it was rather small and arose from the olecranon between the long abductor of the fifth digit and the internal anconeus. Its tendon expanded to cover the three medial digits and adjoining part of the carpus.

It is difficult to see why Murie and Miller both made the mistake they did in their treatment of this muscle. For *Arctocephalus*, *Eumetopias*, and *Obobenus*, the palmaris longus of Miller and primus of Murie was really a superficial division of the digitorum profundus, tentatively termed by me a flexor pollicis longus because of its position. Innervation is by the median nerve, and although this fact

was inferentially mentioned by Miller, he did not take into account that such innervation prevents affinity with the palmaris. There was intimate attachment of its tendon to the palmar fascia, indubitably, and ultimately the fusion will probably be complete, but careful dissection proves that the main portion of the tendon extends to the pollex. Miller's palmaris superficialis and Murie's secundus division were merely the antibrachial extension of the pectoralis, which also had intimate connection with the palmar fascia. I found nothing whatever in the *Phoca* that could correspond with Miller's second head of the palmaris for the same genus. His first head is very similar to the muscle as I found it.

M. pronator teres (figs. 9, 10, 22, 23) lay mediad of the biceps and brachialis. In the *Zalophus* it arose in intimate relation with the flexor carpi radialis from the proximo-caudal margin of the medial epicondyle of the humerus. In the *Phoca* it was from practically the same spot. Insertion in both was upon the radius from near the bicipital rugosity to just distad of the process or angle near the center of its radial border.

The ulnaris and radialis muscles of the Mammalia are usually rather uniform in their locations, but the digitorum muscles—especially the flexors—are annoyingly in the habit of occurring in a great number of combinations. In many cases these are of such a nature that it is unwise to place too much reliance upon the homology as indicated by the nomenclature employed, for in this case the innervation proves to be of little or no aid. Not only does origin vary, but the tendons of insertion are often unreliable as criteria for nomenclature—a muscle homologous with a pollicis may not reach the thumb, or a digiti quinti the fifth digit. The pinnipeds have these flexor muscles of such a sort, and I deem it eminently wise not to refer to the muscular divisions by name but by number, for they are not now to be homologized with any certainty.

M. flexor digitorum communis (figs. 9, 10, 22, 23) in the *Zalophus* consisted of four separable elements, while in the *Phoca* there were three which were separable only at origin.

Caput 1 (figs. 10, 22) in the *Zalophus* was a part of Murie's flexor sublimis digitorum in *Eumetopias.* It arose upon the ulna from caudo-mediad of the sigmoid cavity, passed distad directly superficial to the second division and split into three branches which went to the three lateral digits. The one to the third proved to be double, however, and there seemed to be a broadening of the tendon in the direction of digit 2, possibly indicating the relic of a former branch at this point. These three tendons were the most superficial of any going to their respective digits, the one to the fifth ultimately passing superficial even to the lateral palmaris longus branch. (See fig. 22.)

Caput 2 (figs. 9, 10, 23) in the *Zalophus* was the second part of the flexor sublimis of Murie for *Eumetopias*. It arose from the medial epicondyle of the humerus and from the medio-radial border of the ulna from just distad of the coronoid to within a short distance of the end of the shaft. Its short tendon partly fused with the deep surface of that of the first division and when dissected free it was found to go to digit 4 only. In *Eumetopias* the two heads of the flexor sublimis joined and the tendon sent branches to the four lateral digits. In this as in *Zalophus* the tendons of the first two divisions were entirely separable from those of the third division. In *Arctocephalus* this part of the flexor complex was single and there was fusion of the tendons with those of the third division.

Caput 3 (figs. 10, 22) in the *Zalophus* and Murie's flexor profundus for *Eumetopias*, arose over the medial radius between the biceps, pronator teres, interosseous membrane, and to within a short distance of the distal end of the shaft. Its tendon sent branches to the first three digits. In *Eumetopias* origin was from both the ulna and radius, and two tendons extended to the pollex, two to the index, and one to digit 3.

Caput 4 (figs. 9, 22) in the *Zalophus* was a flexor pollicis longus, innervated by a branch of the median nerve and homologically a division of the flexor profundus, though whether morphologically the same division of this muscle as its analogue in human anatomy is not known. For *Eumetopias*, with origin the same, Murie termed it palmaris longus primus, he believing that its tendon ended in the palmar fascia. Of course, such may actually have been the case in that genus, but the condition in *Zalophus* proves that it is a part of the flexor communis. Origin was from the medial epicondyle adjoining the flexor carpi radialis. Its tendon passed in the superficial flexor layer and near the base of metatarsus one it divided into two, both branches inserting upon the pollex—presumably upon its first phalanx.

In *Arctocephalus* this complex was considerably different. It arose by three heads which Miller termed as follows: A flexor sublimis, from the medial epicondyle with tendon fusing with that of the next; a flexor profundus, from the medial surface of the proximal ulna; and a flexor pollicis longus, from the medial surface of the shaft of the radius and slightly from the ulna, which joined the common tendon of the flexor profundus, and this went to all five digits. For *Odobenus* Murie reported it still different, with the sublimis and profundus bellies partially fused, and a flexor pollicis radiad. All of these were conjoined to a broad tendinous sheet with five branches to the digits. The three divisions named are analogous

to those of man, but there seems to be some doubt as to whether they are homologous.

In the *Phoca* the flexor digitorum communis arose by three heads. *Caput a* had origin from the medial epicondyle below the flexor carpi radialis; *caput b* had origin from the whole of the medial surface of the olecranon and from two-thirds of the shaft of the ulna; while *caput c* originated from the radius, upon the ulnar side of the pronator teres insertion. The three heads joined to form a very broad tendinous band which split into five branches, one going to each digit. This was substantially the same as conditions in the *Phoca vitulina* of Miller, who called caput *a* the flexor sublimis, caput *b* the flexor profundus, and caput *c* a flexor pollicis longus. His nomenclature may possibly be correct and the divisions seem to be homologous with those of *Arctocephalus*, but they certainly are not with those bearing the same terms for *Eumetopias*, as designated by Murie.

M. flexor carpi radialis (figs. 9, 22, 23) lay upon the ulnar side of the pronator teres. It arose in both animals from the medial epicondyle. In the *Zalophus* its tendon inserted chiefly upon metacarpus one deep to that of the supinator longus, but a tenuous branch went also to metacarpus 2. In the *Phoca* insertion was also upon metacarpus 1 and 2, and probably 3 as well. Miller reported three branches to the three metacarpals in *Phoca* and three in *Arctocephalus* to the first two metacarpals and the ligament between the trapezium and trapezoid. In *Eumetopias* insertion was upon the first metacarpal only.

M. pronator quadratus (fig. 9). Murie found this muscle in *Odobenus* but not in *Eumetopias*, while Miller did not find it at all in *Phoca* or *Arctocephalus*. In the *Zalophus* it was represented by a few fibers upon the flexor side of the interosseous membrane, while in the *Phoca* it was weakly though indubitably present.

M. flexor carpi ulnaris (figs. 10, 21, 22, 23) in the *Zalophus* was fused with the palmaris longus. It was the ulnaris portion of the latter muscle, however, that was attached to the pisiform. In the *Phoca* it was located between and deep to the palmaris and long abductor of digit 5, and was a robust muscle. Origin was from the medial olecranol border, with a rather complex insertion, for although there was attachment to the pisiform as usual, the main thread of the tendon continued to metacarpus 5. In addition a tendinous fascia was given off mediad, this forming a second and deeper palmar fascia, and this curved deep and laterad to form part of the thick sheath of the flexor digitorum communis. In *Arctocephalus* and *Eumetopias* it was very similar to that of *Zalophus*. In his *Phoca* Miller reported the same condition found by me in the same genus, save that he made

no mention of complexity in connection with the sheath of the flexor communis.

M. abductor digiti quinti longus (figs. 10, 21, 23) was really a flexor and was served by the ulnar nerve. Its homology is not certain but it seems probable that it may be a division of the flexor carpi ulnaris. It was present in *Phoca* only and arose by aponeurosis from the ulnar termination of the olecranon and its tendon inserted upon the first phalanx of digit 5.

In the *Zalophus* the antibrachial extension of the pectoralis must be included with the flexors of the lower arm. In the juvenal specimen this detail proved puzzling, for after the part of the pectoral aponeurosis inserting upon the deltoid ridge had been removed and the subdermal tissue of the manus dissected free, there remained an apparently distinct structure wth muscle fibers attached arising from the slight ridge extending from the deltoid crest to the medial rim of the trochlea. This emerged from between the biceps and the brachialis, and then fused with an extensive and touch sheet of fatty fibrous tissue covering the radial border of the forearm and metacarpus 1. With this were associated dark fibers apparently muscular in character. In Figure 19 this detail is shown as encountered in this specimen after removal of the part of the pectoral inserting upon the deltoid crest, except that the fibrous tissue extending farther upon the cranio-lateral part of the forearm is represented as having been cut away. In a fresh, adult female, however, it was at once seen that this was a part of the deep pectoral, which, in a tendinous sheet, inserted upon the humerus for the entire length of its shaft, extending quite to the pollex, and with it was associated a thick, fatty, fibrous layer, entirely nonmuscular in this adult, that was most extensive over the anterior or radial border of the arm and acted not only as a buffer or shock absorber, but materially broadened the forearm. The fleshy part of the pectoralis that covered the proximal part of the medial forearm was erroneously designated as a superficial layer of the palmaris longus by Murie for *Eumetopias*, and by Miller for *Arctocephalus*.

The extensors of the antibrachium were as follows:

M. extensor digitorum communis (figs. 9, 10, 20, 21) was the most superficial of the forearm extensors, and arose in a thin sheet from the lateral epicondyle of the humerus. Its tendon passed beneath the dorsal carpal ligament close to that of the extensor pollicis longus and in both animals a branch was sent to each of the four lateral digits. This is Miller's primus division of this muscle in his *Phoca*. In *Arctocephalus* he stated that it split into two slips, one being the same as I found the extensor communis in *Zalophus* and the second constituting an extensor minimi digiti. In *Eumetopias* and

Odobenus the slip representing this muscle split into three tendons passing to the three middle digits.

M. extensor digitorum lateralis (figs. 9, 10, 20, 21) is, in most mammals, a more fitting name for this muscle than its homologue, extensor digiti quinti proprius. In the *Zalophus* it was located between and partly deep to those of the extensores communis and carpi ulnaris. It arose from the distal part of the lateral epicondyle and the lateral radial ligament in such a position that tension could be applied only during flexion of the forearm. It was a weak and slender muscle whose fine tendon split first into two, the lateral branch going to the lateral border of the fifth metacarpal. The medial branch again divided into two, sending one tendon to the medial side of metacarpus 5 and another to the adjoining border of the fourth. In the *Phoca* this muscle was quite complex and occurred in three parts which were not completely divisible proximad. Origin was considered to be from the lateral epicondyle only, although there was quite firm attachment to the capsule of the joint over the head of the radius. Three tendons developed from as many muscular slips which passed ectad of the long extensor of the pollex. The more ulnar of these split into two branches which extended to metacarpals 4 and 5. The more radial also split into two, extending to metacarpals 2 and 3, while the deeper (not shown in fig. 21) inserted upon the ulnare. For this muscle in *Eumetopias* Murie recognized two divisions, equal together to my one. One was a minimi digiti, with tendons to digits 4 and 5, and the other a medii digiti, with tendons to digits 3 and 5. In *Obodenus* these tendons went only to digits 4 and 5. Miller considered that for *Arctocephalus* there was a single head of origin for the communis digitorum and minimi digiti. The latter divided into three main branches going to metacarpals 4 and 5. For *Phoca*, Miller termed this division the extensor communis secundus, mentioning no divisions of the muscle itself but that it split into four tendons, passing to the four lateral metacarpals.

The structure referred to above as the lateral radial ligament deserves mention. It occurred in the *Zalophus* only, as a broad, tough band extending from the lateral epicondyle over the lateral aspect of the radius to somewhat distad of its middle. It covered the supinator brevis and was continuous along its border with the interosseous membrane where this adjoined. Its function was as its name implies—to add great strength to the joint. It was not an outgrowth of the normal capsular ligament of the elbow, for it not only had some vestige of muscle fibers associated with it but seemed to be served by the dorsal interosseous nerve, which indicated that it may have been a relic of some primitive division of the common extensor group of the digits. No mention was made of such a structure in other eared seals.

M. extensor metacarpi pollicis (figs. 10, 20, 21) arose in the *Zalophus* from the whole of the fossa of the lateral ulna that was situated upon the radial side of its prominent lateral ridge, and extended in origin two thirds the length of the shaft. It ran obliquely across the radius and its tendon passed through the large groove upon the cranio-lateral termination of the radius. It then passed to a double insertion, the first to the medial base of metacarpus 1, and the other to the first phalanx of the same digit. In the *Phoca* it arose from the whole of the lateral face of the olecranol plate save the extreme ulnar tip. Its tendon inserted as normal upon the base of metacarpus 1. This was termed extensor ossi metacarpi pollicis by Murie and Miller. From the former's description, insertion in *Eumetopias* and *Odobenus* seems to have resembled that in my *Phoca*, but the tendon was much weaker in the latter animal.

M. extensor pollicis longus (figs. 10, 20, 21) in the *Zalophus* arose from that part of the fossa on the lateral ulna that was situated upon the ulnar side of its prominent ridge. Its very broad tendon extended obliquely across the carpus and was inserted upon the dorsum of the first phalanx of the pollex. In the *Phoca* it arose from the ulnar tip of the lateral olecranon and for some little distance distad, while insertion was as in *Zalophus*. For *Eumetopias* Murie termed this muscle extensor pollicis et indicis but noted no differences, and it is Miller's extensor primi internodii pollicis. In the latter's *Phoca vitulina* origin was from the posterior third of the ulna.

M. extensor carpi ulnaris (figs. 9, 10, 20, 21) in the *Zalophus* appeared very similar in its proximal portion to the extensor communis. It arose by aponeurosis from the radial two-thirds of the olecranol border of the ulna beneath the lateral anconeus. Its rather slender tendon passed to the lateral manus and was inserted upon the lateral border of metatarsus 5. In the *Phoca* origin was from the lateral epicondyle of the humerus, while insertion was normal as in *Zalophus*.

M. extensor carpi radialis (figs. 9, 10, 20, 21) was single in its muscular portion and arose from just dorsad of the lateral epicondyle proper. It extended next laterad to the supinator longus and its tendon was seen to be double. In the *Zalophus* these are doubly inserted into the lateral border of metacarpus 1 and the medial border of metacarpus 2. In the *Phoca* one tendon went to metacarpus 2 and the other sent two branches to metacarpals 2 and 3 respectively. As this insertion was different from anything reported for the genus, I was careful to verify it. Miller wrote that in *Phoca vitulina* insertion was upon the first and second metacarpals, while in *P. barbata* it was upon the second only.

M. supinator longus (figs. 9, 10, 20, 21, 23) in the *Zalophus* was specialized. Origin was from the more caudal portion of the lateral shaft of the humerus extending quite to the head and partially between the brachialis and triceps. This excepts the deltoid crest, from the distal termination of which arose but a few fasciculi of this muscle. It then passed between the brachialis and extensor carpi radialis and was joined by the more distal part of the deltoid. Its tendon was inserted upon the most prominent part of the radial aspect of the distal termination of the radius, just deep to the tendon of the extensor metacarpi pollicis. In the *Phoca* origin was much more restricted and more caudad, and there was no connection with the deltoid. Murie stated that in *Eumetopias* this muscle had two heads, the second from the deltoid crest, but I judge that there was little difference from conditions in the *Zalophus*. From the description of *Arctocephalus* the origin in this animal was more extensive.

M. supinator brevis (figs. 9, 10, 20, 21) had its usual complex origin, chiefly from the capsule of the elbow joint, but also upon the lateral condyle of the humerus as indicated. (Fig. 9.) Insertion in both animals was upon the cranio-lateral part of the radius from its head to the pronator teres angle.

The short muscles of the manus of these two families of pinnipeds were adequately investigated by Murie and Miller, and as they are not particularly pertinent to the present report, they are here omitted.

MUSCLES OF THE POSTERIOR LIMB

MUSCLES OF THE HIP

The hypaxial muscles or psoal complex presented no especial difficulties in *Zalophus*, but in the *Phoca* they were extremely closely associated, peculiar, and withal so tender that nice dissection was entirely out of the question. Miller found these muscles different in each phocid which he dissected, his descriptions are too involved, and at least one error is indicated, for his magnus did not go to the limb. His contribution is therefore of slight aid in this respect, nor am I able to homologize things entirely to my own satisfaction.

M. psoas minor (figs. 11, 24) in the *Zalophus* was rather small and arose apparently from all the lumbar vertebrae, but craniad the association with the quadratus lumborum was so close that one can not distinguish between the two muscles with certainty. A very slender separate head also arose from the centrum of the last lumbar, joining the remainder by a small tendon. The whole became stoutly tendinous and inserted upon the pectineo-psoal process of the innominate. In the *Phoca* the part that indubitably represented this muscle was

the most medial of the divisions and also small. It arose apparently from the last three lumbars and inserted slenderly upon the pectineal process. Conditions have been essentially similar in the other pinnipeds dissected, including a small *Phoca vitulina* by Miller; but in the case of a large specimen of this species the same author stated that this muscle was enormous and much larger than the psoas major, which seems to indicate that an error was made in either one or the other.

M. psoas magnus (figs. 11, 12, 13, 24) in the *Zalophus* was less robust at the original but larger at the insertional end than the minor

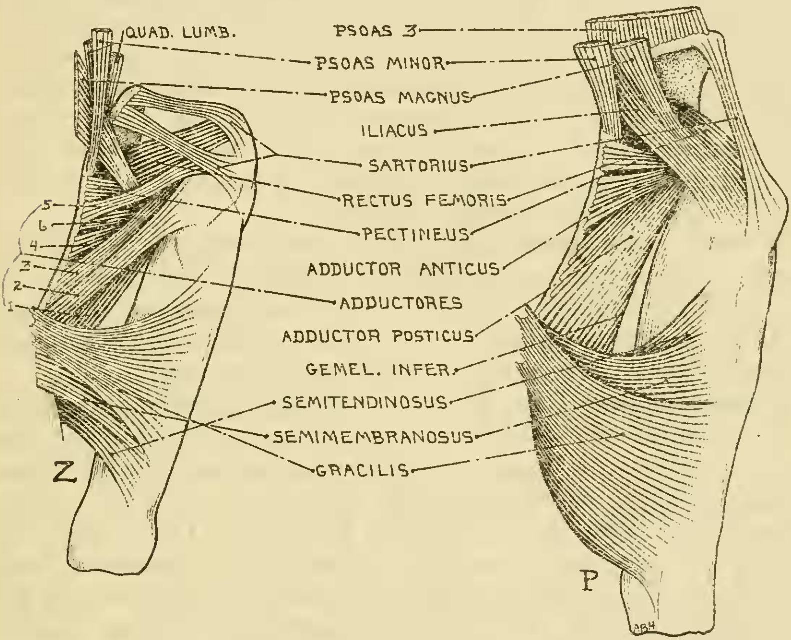

FIG. 24.—VENTRAL ASPECT OF THE MUSCLES EXTENDING FROM THE INNOMINATE BONE (STIPPLED) TO THE POSTERIOR LIMB OF ZALOPHUS (*Z*) AND PHOCA HISPIDA (*P*)

division. Origin was from the last two lumbars and the extreme anterior sacrum. It passed beneath (dorsad of) the minor and between the rectus femoris and pectineus, and inserted tendinously upon the lesser trochanter. It is difficult to understand the conditions in Miller's *Arctocephalus*, or in his other pinnipeds for that matter. In my *Phoca* there was no difficulty about the insertion which was with the iliacus upon the medial tuberosity of the tibia. In this tender specimen, however, origin was entirely inseparable from a great mass of muscle extending from the thorax to insert chiefly upon the ventral part of the medio-cranial face of the ilium. About any such insertion in his specimens Miller mentions nothing.

A small slip also separated from this mass to insert upon the psoas process of the ventral ilium. The homology of this large mass of muscle is very uncertain, but it may provisionally be termed psoas tertius. (Figs. 11, 24.)

Murie considered that in *Eumetopias* either the two psoas muscles had fused or the true psoas minor was absent, the two muscles of this group therefore consisting of a psoas and an iliacus. For *Odobenus* he said that the two psoas were closely united, and inserted by a common tendon upon the ilio-pectineal eminence—an interpretation that is open to question.

M. iliacus (figs. 11, 12, 13, 24) was not entirely distinct. In the *Zalophus* it was very small, arising from the ventral border of the ilium in intimate relation with the final slip of the quadratus lumborum. It inserted with the psoas magnus upon the lesser trochanter. In the *Phoca* its fibers were inseparable from the part of the psoas tertius which joined the ventral ilium, while insertion was with the psoas magnus upon the medial tuberosity of the tibia. This muscle seems invariably to be present in pinnipeds.

M. tensor fasciae femoris (figs. 12, 17) arose from the lumbodorsal fascia, in the *Zalophus* reaching the middorsal line over the last two lumbar vertebrae. In the *Phoca* the exact bounds of the muscle could not be so well defined because of the condition of the specimen. Insertion in both was upon the lateral part of the patella.

M. gluteus maximus (figs. 12, 16, 17) in the *Zalophus* had origin continuous craniad with the biceps femoris over the spines of the three sacral vertebrae. It passed over the proximal part of the greater trochanter, to be inserted upon the disto-lateral part of the same, but not appreciably onto the shaft of the femur. In the *Phoca* this muscle was very heavy, indeed, and arose by aponeurotic fascia over the middorsal space included between all four sacral and first two caudal vertebrae. It quickly converged to a tendinous insertion along the entire lateral border of the shaft of the femur from the lateral condyle to the distal part of the greater trochanter, although over the middle of this space there seemed to be no actual attachment to the bone. In both *Eumetopias* and *Arctocephalus* two heads were reported, but the separation seems to have been incomplete. At any rate, insertion was upon the shaft of the femur as well as the greater trochanter, thus resembling the condition in my *Phoca* rather than the *Zalophus*. Miller wrote that in *Phoca vitulina* there were also two heads and that one of them arose from the ilium.

M. gluteus medius (figs. 11, 12, 16, 17) in the *Zalophus* arose from the anterior border of the ilium, and this part was not covered by the gluteus maximus. Near the insertion it was separable, except at its ventral border, into two thin sheets, these forming a V-shaped tendinous attachment to the greater trochanter. In the *Phoca* this

muscle and the pyriformis of the present specimen were inseparable, the two parts being distinguished only by a faint line presumably between them ectomediad. Origin of the two together was from all but the ventral part of the "lateral" surface of the ilium practically to the acetabular border and thence upon the sacrum over the second sacral vertebrae, and upon the ridge extending to the transverse plate of the third sacral. Insertion was almost entirely fleshy upon the flattened part of the greater trochanter. In *Eumetopias* Murie reported origin as also from the sacrum, presumably the spines.

M. gluteus minimus (figs. 11, 12, 16) in the *Zalophus* seemed to be partially divisible, along its dorsal border only, into three slips. It arose from the lateral surface of the cranial half of the ilium and from two-thirds of the vertebral border, with a few fibers from the ventral surface of the ilio-sacral ligament. Insertion was strongly upon the greater trochanter. In the *Phoca* this muscle was entirely covered by the medius. It arose from the ventral fossa and ridge adjoining the "lateral" surface of the ilium. Insertion was somewhat tendinous upon the dorso-medial part of the greater trochanter.

M. gluteus quartus (figs. 11, 12). No slip representing this muscle was mentioned by either Murie or Miller. In my *Zalophus*, however, it could not be ignored. It was very slender and arose from the ilium craniad of the femoral process and with attachment also to the tendon of the rectus. It passed just superficial to the latter muscle to insert upon the greater trochanter in the angle between the insertions of the glutei medius and minimus.

M. pyriformis (figs. 12, 16) in the *Zalophus* was easily separable from the gluteus minimus, caudad of which it lay. It arose from the last two sacral vertebrae beneath the caudal portion of the ilio-sacral ligament, and converged to a tendinous insertion upon the greater trochanter. In the *Phoca*, as mentioned, this muscle was inseparable from the gluteus medius. In *Phoca vitulina* Miller separated it with care.

After disposing of the gluteal-pyriformis mass, the complex consisting of the gemelli, obturator internus and adductor posticus appeared in the seal as consisting of a single, strong, well-rounded muscle and much care was necessary in its dissection, partly, of course, because of the extreme tenderness of the fibers.

M. gemellus superior (figs. 11, 12) lay next caudad to the pyriformis. In the *Zalophus* it was a much weaker muscle, arising from the superior border of the ischium just caudad of the acetabulum. Insertion was upon the caudal aspect of the greater trochanter dorsad of the obturator fossa. In the *Phoca* origin was relatively farther caudad, and its tendon joined the other which, in turn, joined that of the obturator internus inserting into the trochanteric fossa of the

femur. Murie stated that in *Eumetopias* origin was from the sacral vertebrae, which seems unlikely.

M. obturator internus (figs. 12, 16) arose from the inner border of the obturator foramen and its membrane, passed over the dorsal border of the ischium between and in close association with the two gemelli, and inserted by the usual tendon into the trochanteric fossa of the femur.

M. gemellus inferior (figs. 11, 12, 16, 24) in both animals arose from a similar area upon the dorsal border of the ischium—roughly the second quarter of the distance from the acetabulum to the caudal border. In the *Phoca*, however, there was in addition a strong tendon arising from the bicipital process and disappearing in the substance of the muscle. In the *Zalophus* insertion was upon the side of the greater trochanter, between the obturator internus and quadratus femoris. At first glance it seemed to be a part of the latter muscle. In the *Phoca* its tendon joined the insertion of the obturator internus. For *Eumetopias* insertion was given as between the greater and lesser trochanters. Miller referred to this muscle in parts of his text but did not describe it.

M. quadratus femoris (figs. 11, 12, 16) in the *Zalophus* arose from the dorsal half of the caudal border of the ischium, bounded dorsad by the gemellus inferior, ventrad chiefly by adductor 1, and mediad by the obturator externus. Insertion was along the entire latero-caudal border of the femur. In *Arctocephalus* insertion was said to be upon the "lower half of the posterior border of the great trochanter." For *Eumetopias* Murie gave insertion as the outer side of the lesser trochanter. The muscle is absent in the Phocidae.

M. obturator externus (figs. 11, 12) in the *Zalophus* arose not just from the border of its foramen, but from a considerable area of bone caudad and ventrad, and from all but the dorsal part of the obturator membrane. Insertion was tendinous near the disto-caudal part of the greater trochanter. In the *Phoca* origin was much more restricted. It arose from the obturator membrane only over its dorsal and cranial parts, from the bone anterior to the obturator foramen, and from the dorso-cranial part of the pubis, the latter part of the muscle having almost the appearance of a separate slip. Insertion was partially tendinous into the obturator fossa of the femur. In *Eumetopias* insertion was said by Murie to be onto the lesser trochanter, while in *Mirounga* insertion was upon the greater trochanter; but in this Miller was probably mistaken, as he was, at least for *P. hispida*, when he stated that the adductors are absent in the Phocinae, for the adductors constitute the ectal part of his obturator externus, and he evidently missed the deeper and very small latter muscle.

MUSCLES OF THE THIGH

There was evident a decided tendency toward fusion of the gracilis, semimembranosus, and semitendinosus of *Phoca*, and the three together formed a great muscle mass with a single prime function. No such tendency was found in *Zalophus*.

M. semimembranosus (figs. 11, 13, 24) of *Zalophus* occurred in two parts. The posterior (really the inferior) arose from the caudal border of the ischium adjoining the symphysis and the origin of the gracilis. Insertion was narrow and fascial beneath the caudal border of the gracilis. The anterior division, of about the same size, arose from the caudal border of the ischium dorsad of the origin of the posterior part. Fascial insertion upon the cranial border of the tibia was entad of the cranio-dorsal border of the gracilis and was entirely hidden by the latter. In the *Phoca* this muscle was single and arose along the caudal border of the ischium, the more caudal part being incompletely separable from the gracilis, under cover of which muscle it extended to a fleshy insertion not directly upon the tibia but upon the heavy aponeurosis investing the ventral belly of the semitendinosus. For both *Eumetopias* and *Odobenus* Murie called this muscle semitendinosus. In *Arctocephalus* it was single, while Miller reported it double for *Phoca*.

M. semitendinosus (figs. 11, 13, 16, 17, 24) in the *Zalophus* arose from over the spines of the third to sixth or seventh caudal vertebrae, with fascial insertion upon the distal quarter of the shaft of the tibia (not including the malleolus). In the *Phoca* it occurred in two parts which were entirely distinct at origin but apparently fused more distad. The posterior division was the more superficial and much the larger. It arose robustly from the transverse processes of the first three caudal vertebrae. The anterior division arose by tendinous fascia from the caudal border of the ischium along an area adjacent to the semimembranosus but not reaching the dorsal spine. The insertional end of both parts together developed a stout aponeurosis attached along the cranial border of the tibia and the hamstring tendon. This is the muscle which Murie termed semimembranosus. It was single also in *Odobenus*, *Eumetopias*, and *Arctocephalus*.

In both animals the aponeurosis of insertion of these hamstring muscles ended in the tough fascia and connective tissue over the heel. In *Phoca* especially it may be said to end in a sort of ligament which extended from the head of the fibula to the most prominent part of the external malleolus, and there was also substantial anchorage in the fibrous tissue beneath the calcaneal tendon.

M. biceps femoris (figs. 11, 12, 13, 16, 17) in the *Zalophus* occurred in three main parts. The more superficial portion of the long head was

indeed a very remarkable muscle, origin extending from the spine of the second to that of the seventh caudal vertebrae. The fibers extended caudo-laterad to a tough sheet of aponeurosis covering the side of the lower leg and stretching from the outer condyle of the femur, the adjoining part of the tibia, and to the distal extremity of the shank. In *Eumetopias* and *Odobenus* origin was a trifle farther caudad. A posterior head was very narrow and arose under the caudal border of the main muscle, but its insertion was merely a distal continuation of that of the main mass. This may be the muscle termed by Murie a levator ani. The socalled short head of the biceps was but a couple of centimeters in width and arose partly from the transverse process of the second sacral vertebra and partly from the sacro-iliac ligament. It inserted upon the aponeurotic sheet investing the dorsal border of the distal fibula.

In the *Phoca* the biceps occurred in two divisions. The superficial arose by a strong, tendinous origin from the dorsal spine of the ischium. It spread fanwise to a fascial insertion over the proximal seven-eighths of the lateral part of the tibia. It is thus seen that in the *Zalophus* this muscle was in the form of a parallelogram, closely binding the shank to the vertebral column, while in the *Phoca* it was in the form of a triangle with pivotal apex upon the ischium, theoretically permitting much more freedom of movement. The deep division of the biceps of the *Phoca* was narrow and strap-shaped, with fleshy origin from the transverse plate of the third sacral vertebra, and aponeurotic insertion over the distal fibula. This corresponds with the short head of *Zalophus*.

Murie termed the short head in *Eumetopias* the sacro-peroneus, and Lucae designated the heads as ischio-tibialis and sacro-fibularis. In *Arctocephalus* there were three divisions, much as in *Zalophus*.

M. sartorius (figs. 11, 12, 13, 16, 17, 24) in the *Zalophus* occurred in two distinct slips. The proper one was very slender, arising from the ventral angle of the iliac border with insertion upon the medial patella partly deep to the tensor fasciae. The second arose from the cranial part of the ventral border of the ilium and had fascial insertion upon the medial tuberosity of the tibia mediad to and continuous with that of the first division. In the *Phoca* it was single, arising from the ventral angle of the ilium with insertion upon the patella continuous with and mediad to the insertion of the tensor fasciae. Miller reported it as single in *Phoca* and double in *Arctocephalus*, and Murie found it single in *Eumetopias* and *Odobenus*.

M. rectus femoris (figs. 11, 12, 16, 17, 24, 25, 26) was a robust muscle arising from the femoral process of the ilium cranio-ventrad of the acetabulum, which is prominent in *Zalophus* but indicated only by a roughened area in the *Phoca*. Insertion was upon the patella deep to the sartorius and tensor fasciae femoris.

The vasti were separable into two divisions only.

M. vastus lateralis (figs. 12, 25, 26) arose from the dorso-cranial part of the greater trochanter and for a very short distance distad along the lateral border. Insertion was upon the lateral patella and slightly upon the capsule of the joint. Miller considered that the vastus externus of all the pinnipeds which he dissected arose from the entire lateral border of the femur, and Murie from the "anterior surface of the femur," but I deem the true origin to be more restricted.

M. vastus profundus (figs. 12, 25, 26) evidently comprised a fused vasti femoris and medius. In the *Zalophus* origin was from practically the entire cranial surface of the femur, and in the *Phoca*, from only the proximal half. Insertion in both was upon the medial patella and adjoining part of the capsule of the knee partly deep to the insertion of the rectus femoris. Miller designated the deeper vastus as the crureus, and Murie, the vastus internus.

The adductors consisted of the following muscles:

M. pectineus (figs. 11, 12, 24) in the *Zalophus* arose from the dorsocaudal slope of the pectineo-psoas process of the innominate and the tendon of the psoas minor adjoining. Insertion was upon the distal border of the lesser trochanter adjoining that of adductor 6. In the *Phoca* origin was longer, from the border of the publis for a short distance directly caudad of the "pectineo-psoas process." Insertion was also fleshy upon the proximo-medial portion of the caudal aspect of the femoral shaft, or close to the corresponding position of the lesser trochanter of *Zalophus*, absent in the *Phoca*. In *Arctocephalus* origin was much as I found it in *Phoca*. Miller considered that this muscle was Murie's adductor brevis primus, and that there was really a second division, termed pectineus for *Eumetopias* and *Odobenus*, and called by Miller for *Arctocephalus* pectineo-superficialis vel femoralis. Both Murie's and Miller's treatment of the pectineo-adductor complex is irrational. There is no good reason, morphologically, for considering that the pectineus has taken upon itself complexity. The pectineus of Murie and the pectineo-superficialis vel femoralis of Miller were, in fact, clearly a subdivision of the true adductor mass.

M. gracilis (figs. 11, 13, 24) in both animals was incompletely double at origin, the two heads being separated, craniad only, by the rectus abdominis. The more ectal arose midventrad, its fibers decussating with those of its antimere, and the more entad from the symphysis and the ischium laterad thereto. Insertion was fascial, in the *Zalophus* along the middle third, and in the *Phoca* the distal half, of the tibia. In the latter animal there seemed to be a slender tendon or ligament developing from this fascia and passing over the medial malleolus and joining the plantar fascia. In *Odobenus* insertion was upon almost the entire shaft of the tibia.

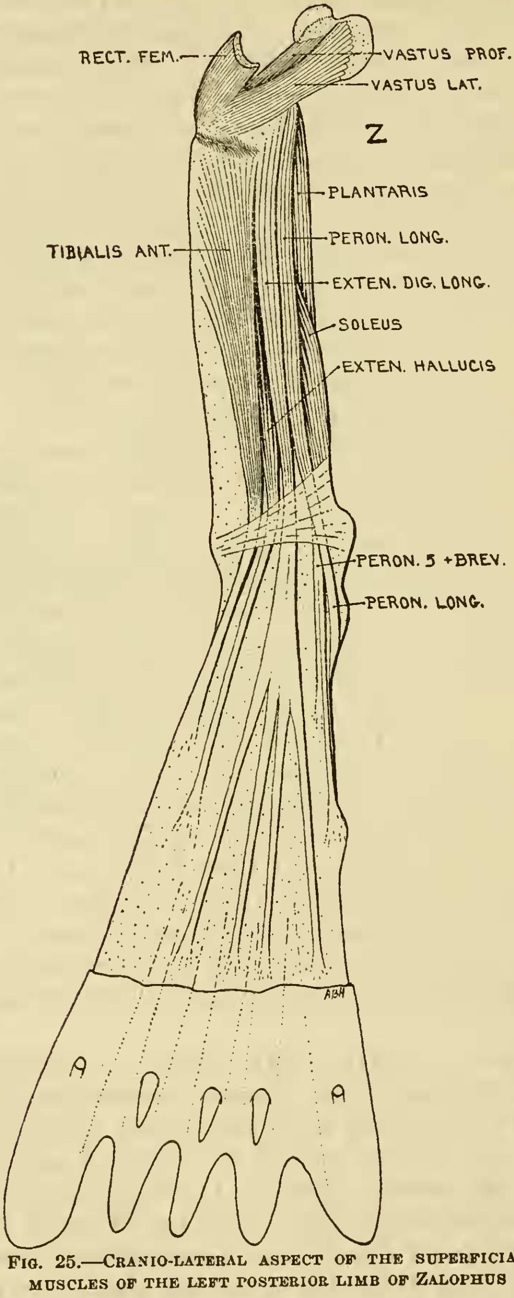

FIG. 25.—CRANIO-LATERAL ASPECT OF THE SUPERFICIAL MUSCLES OF THE LEFT POSTERIOR LIMB OF ZALOPHUS

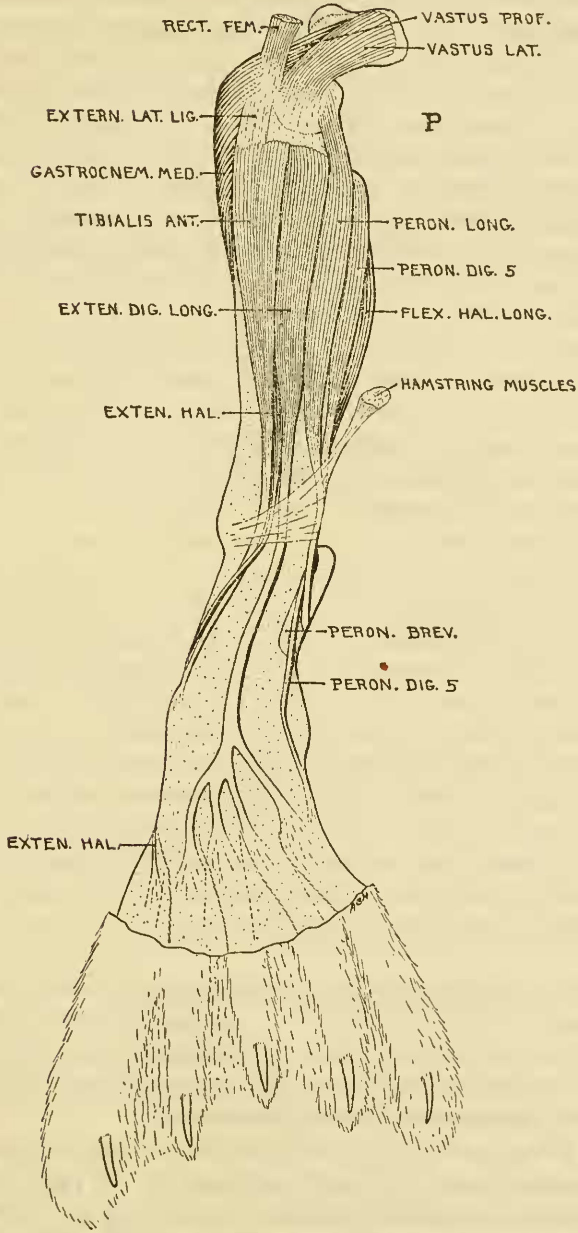

FIG. 26.—CRANIO-LATERAL ASPECT OF THE SUPERFICIAL MUSCLES OF THE LEFT POSTERIOR LIMB OF PHOCA HISPIDA

In no respect, perhaps, does the tendency for subdivision of the muscles of the posterior limb of *Zalophus* and fusion of those of *Phoca* appear more pronounced than in the adductor muscles and certain others near them. The adductors, however, when these show complexity, is one of the groups which it is as yet not only unwise but actually misleading to attempt to homologize too precisely with the human divisions, and we must know far more regarding the lower Mammalia than we now do before such a course can be taken with confidence. The reason for this is that save for a part of the adductor magnus, little can be proved by the innervation, and it is both simpler and more satisfactory to refer to a number of divisions by number. In *Zalophus* I began at the most caudaul division and worked craniad. (Figs. 11, 12, 13, 24.)

Adductor 1 in the *Zalophus* was thin and arose from the caudal border of the ischium between the origins of the semimembranosus anticus and quadratus femoris. It passed laterad to all the other adductors to a fascial insertion over the medial tuberosity of the tibia and onto a slight ridge extending along the distal border of the medial condyle of the femur.

Adductores 2 et 3 were apparently indivisible at origin, which was along the caudal half of the pubis laterad of the symphysis and that part of the ischial border that lay ventrad of the obturator foramen. These two divisions were undoubtedly homologous with at least a part of the true adductor magnus, for the femoral artery passed between their insertional parts. At the middle of the muscle the more ventral fibers separated into a ribbonlike slip—adductor 2—extending to a ridge upon the medial condyle of the femur. The deeper part, constituting adductor 3, inserted upon a long, narrow area stretching over the caudal surface of the femur from the distomedial greater trochanter to a point upon the medial border of the shaft midway between the lesser trochanter and the condyle. On the bone this is indicated by a barely perceptible ridge, corresponding to the usual linea aspera.

Adductor 4 was small and arose from the pubic border just craniad of the origin of divisions 2 and 3. It passed deep (mediad) to both of the last, broadened somewhat and inserted upon a slight ridge extending over the caudal shaft of the femur from distad of the middle of the greater to the lesser trochanter.

Adductor 5 was also very narrow, arising along the pubic border from the pectineo-psoas process to adductor 4. It passed superficial (mediad) to all the other adductors in this area to a fascial insertion over the medial epicondyle of the femur. This is the pectineus of Murie.

Adductor 6 arose from the pubis immediately deep to division 5, and inserted narrowly upon the disto-lateral border of the lesser trochanter.

The much simpler adductors of *Phoca* may be termed as follows:

Adductor anticus (figs. 11, 12, 24) was a small muscle next caudad to the pectineus and of about the same size. Origin was from the border of the pubis and insertion was mediad to that of the pectineus upon the shaft of the femur, but there was no appreciable osteological indication of the fact.

Adductor posticus (figs. 11, 12, 17, 24) was a very broad sheet of muscle arising from the caudal half of the pubic border and over the lateral surface of all of the ischium save the more caudal portion. It converged to an insertion that was largely tendinous upon the prominence upon the femur just laterad of the trochanteric fossa.

Murie indicated that there were six adductors in *Eumetopias*. As already mentioned, his adductor brevis primus is the true pectineus, and what he termed pectineus is my adductor 5. I am unable to determine the exact number of adductor divisions in *Arctocephalus* but judge that conditions were very similar to those in my *Zalophus*. Miller wrote that the adductors are absent in *Phoca*, but it is evident that he mistook the two adductors for the obturator externus and did not dissect deeply enough to encounter the latter muscle, restricted as it is in this genus.

MUSCLES OF THE LEG

M. gastrocnemius (figs. 12, 26, 27, 28) was single in the *Zalophus* and arose from the well-defined ridge upon the medial epicondyle of the femur and the capsule of the joint. It crossed to the outer side of the shank and developed a tendon (first upon its medial border) which was inserted upon the calcaneum. In the *Phoca* this muscle was double. The *medialis* was very heavy, with fleshy origin from the caudal surface of the well developed medial epicondyle. An internal tendon developed upon which the fibers from both bellies of the muscle inserted. The tendon narrowed and was attached to the calcaneum. The *lateralis* was not one-tenth the size of the medial division. It arose by a slender tendon from the lateral epicondyle of the femur, and joined the tendon of the medial division distad of the muscular part.

M. plantaris (figs. 12, 25, 27, 28) in the *Zalophus* was about one-third the size of the gastrocnemius. It arose from the lateral epicondyle of the femur in very intimate relation with, and between, the popliteus and peroneus longus. It passed deep to the tendon of the gastrocnemius, over the groove upon the medial calcaneum, and thence to the plantar fascia. With care two layers of this were dissected free. The more superficial divided into four tendons between the five digits, and each of these again divided, the branches running to the borders of the adjoining digits. The deeper layer also separated into four branches, these constituting sheaths for the flexor

longus tendons extending to the four lateral digits. These last entered the sheaths from their deep sides near the metatarsal-phalangeal joints. In the *Phoca* the plantaris was much larger than the lateral, but smaller than the medial, gastrocnemius. It had an extensive fleshy origin from the caudal surface of the lateral epicondyle, the head being really separable into two parts, one arising from the ridge at this point and the other from the slight furrow adjoining. Its slender tendon passed mediad from beneath the gastrocnemius and over the depression between the calcaneum and astragalus. It then extended not to the superficial layer of the plantar fascia but deeper, to an attachment upon the plantar surface of the flexor hallucis longus. Its tendinous fibers continued, however, apparently to the fourth digit only.

M. soleus (figs. 13, 25, 27) is present in the otariids only. In *Zalophus* it was very thin at origin and robust at insertion. It arose by aponeurosis from the head of the fibula and by muscle fibers from the caudal border of the shaft as well as from the aponeurosis covering the peroneus brevis. Insertion was entirely fleshy upon the dorsal surface of the calcaneal extension deep to the tendon of the gastrocnemius. This muscle was very closely involved with the peronei brevis and digiti quinti. It is lacking in the Phocidae.

M. popliteus (figs. 12, 13, 27, 28) in the *Zalophus* was extensive but thin. Origin was by a tough tendon from the depression between the lateral condyle proper and the condyloid ridge, and by muscle fibers from the capsule of the joint, and was in intimate relationship with the plantaris. The belly expanded as usual and near the insertion, especially proximad, it divided into two thin sheets to allow for the passage of the internal lateral ligament. Insertion was upon the medial border of the shaft of the tibia from a point slightly distad of the head practically to the center of the shaft, but there was no osseous indication of its position. In the *Phoca* this muscle was rather thick but relatively narrow. Its tendon arose from the pit cradiad of the lateral condyle, origin being a bit smaller than in *Zalophus*, and some of the muscle fibers also arose from the capsule of the joint. Insertion was less than 25 mm. in length and at quite some distance from the head.

The flexor and extensor tendons to the digits have a habit, in diverse sorts of mammals, of wandering about, and the homologue of a hallucis or a digiti quinti muscle may be found to extend to some other digit besides the hallux or the fifth digit, respectively. Hence one can not always judge by insertion, nor by origin either, regarding the name of a muscle. When the innervation is not diagnostic the matter may become extremely difficult. Such is the state of affairs concerning the long flexors of *Zalophus* and *Phoca*. The one that extends to the hallux in the former does not do so in the

latter and vice versa. In the former the more medial arose directly superficial to the lateral. My nomenclature is based on the fact that in the *Phoca* the muscle which I term the digitorum longus was located in its normal position mediad to the hallucis, and in both my animals, the digitorum tendon is the one located nearer the calcaneum than the hallucis where they both pass over the heel. It is fully realized that the positions of the tendons at this point could be transposed, but it is necessary to have some criterion and as both muscles are served by the tibial nerve, homologizing by the innervation in such specialized mammals would not be dependable.

M. flexor digitorum longus (figs. 13, 27, 28) in the *Zalophus* arose deep to the popliteus and superficial to the flexor hallucis longus. Its origin was from the caudo-medial part of the head of the fibula and from the strong tibio-fibular ligament which stretched from the head of the latter bone to a point distad three-quarters the length of the tibial shaft, which ligament marked the medial border of the deep fascia of the shank. The tendon from this muscle passed over the more lateral of the two grooves upon the medial border of the caudal tibia, expanded and joined the tendon of the hallucis longus upon its deep surface. The two layers could be dissected apart, however, when it was seen that the digitorum longus sheet split into three branches, these going, respectively, to digits 1, 3, and 4. In the *Phoca* this muscle was considerably smaller than the flexor hallucis but was still a robust muscle. Origin was fleshy from the tibial side of the head of the fibula and from the adjoining border of the posterior tibial fossa as far as the internal lateral ligament. The tendon passed caudad of the internal malleolus and broadened as it extended deep to, and became fused with, the hallucis longus. After careful dissection it appeared that branches of this tendon extended to digits 2, 3, and 4.

This is Murie's flexor longus hallucis—a fact not mentioned by Miller—and its origin was simlar to *Zalophus*, but the precise insertion is not clear. Miller considered it in the same light as I do for *Phoca* at least, but I can judge little regarding his description of conditions in *Arctocephalus*.

M. flexor hallucis longus (figs. 13, 26, 27, 28) is a somewhat ambiguous name as far as concerns *Zalophus*, but for this genus flexor fibularis would be no better. In the *Zalophus* it arose deep to the flexor digitorum longus from the caudal part of the tibial border of the fibula and from the interosseous membrane, but at no point did fibers quite reach the tibia. The tendon then passed over the heel between those of the plantaris and digitorum longus, expanded, and formed the more superficial layer of the sheet common to this muscle and the digitorum longus. Further dissection showed that it split into but two branches, which extended respectively to digits 2 and 5. The

tendons of the two long flexors which ran to the four lateral digits entered from the deep side into four sheaths which stretched from a part of the plantar fascia, as mentioned elsewhere. In the *Phoca* this was an exceedingly robust muscle. It arose from the caudal head of the fibula and from two-thirds of this aspect of the shaft, as well as to a slight extent from the fibular part of the interosseous membrane. Muscle fibers ceased some 30 mm. proximad of the heel and the very broad tendon—the heaviest of the foot—passed over the groove upon the greatly specialized posterior process of the astragalus, in this animal actually longer than that of the calcaneum. The tone of this muscle and the form of astragalus—giving the action of a regular tendo calcaneus—is all that prevents the foot from assuming a platigrade position. The tendon of the flexor hallucis, after appearing upon the plantar surface, broadened and passed between the tendons of the plantaris and flexor digitorum longus, and partly fused with the latter tendon ectad. It split apparently into four branches, these going to digits 1, 3, 4, and 5. The one to the hallux again split, one branch extending to the dorsum and the other to the lateral side of this digit. This muscle is the flexor longus digitorum of Murie, although Miller evidently failed to notice the fact. The latter's descriptions are very involved, and as he failed to dissect apart the two layers of tendons, no differences of significance can be noted.

M. tibialis posticus (figs. 13, 27, 28) in the *Zalophus* had fleshy origin from the extreme medial part of the head of the fibula, from the fibulo-tibial ligament mentioned under the flexor digitorum longus, and from the entire posterior tibial fossa as far as the distal quarter of the shaft. Its very large tendon passed over the most medial of the two grooves upon the posterior aspect of the tibia, down the medial border of the tarsus and metatarsus, and inserted broadly upon the terminal phalanx of digit 1, this acting as an abductor of the digit. Embedded in the tendon just mediad of the proximal part of tarsale 1 was the tarsal sesamoid bone. In the *Phoca* the flexor digitorum longus covered all but the medio-distal border of this muscle. It was broad but thin and arose chiefly from the posterior tibial fossa for almost three-fifths of the length of the bone, from the interosseous membrane mediad to the flexor hallucis longus, and from the medial head of the fibula. Its rather small tendon passed over the groove caudad to the medial malleolus and inserted upon the lateral centrale. Miller evidently followed the tendon with greater perseverance than I employed and ascribed to it considerable complexity in its attachments over a limited area.

M. tibialis anticus (figs. 13, 25, 26) was the most medial of the muscles of the front of the shank. In *Zalophus* it was rather small and arose from the head of the tibia, from the proximal half of its shaft,

and from the deep fascia covering the extensor hallucis. Its broad tendon passed mediad to an insertion upon the medial margin of metatarsus 1. Origin in the *Phoca* was very similar, being from the better defined anterior tibial fossa and slightly from the adjoining interosseous membrane. Its tendon passed through the deep tibial groove upon the front of the instep, went deep to the extensor hallucis tendon and inserted upon the medial border of the base of metatarsus 1, as in *Zalophus*. There were said to be two tendons in *Eumetopias*, the second inserting upon the first tarsale.

M. extensor hallucis (figs. 13, 25, 26) was a weak muscle in the *Zalophus* arising from the interosseous membrane and slightly from the adjoining borders of both tibia and fibula. Its tendon passed over the instep between those of the tibialis anticus and extensor digitorium longus to insert upon the base of the first phalanx of the hallux. In the *Phoca* its origin was from the proximal part of the cranial ridge of the fibula. It lay mostly deep to the extensor digitorum longus and its slender tendon passed over the instep just laterad to that of the tibialis anticus. It then crossed superficial to the last and ventrad of the base of the first metatarsal, after which it extended dorsad once more to insert upon the lateral side of the dorsum of the first hallucial phalanx. This was said to be of unusual volume in *Eumetopias*.

M. extensor digitorum longus (figs. 12, 13, 25, 26) in the *Zalophus* arose very slightly from the lateral epicondyle of the femur, from the capsule of the joint adjoining, from a small area over the part of the tibial head adjacent to the fibula, and from two-thirds of the cranial border of the fibular shaft. In addition the deeper fibers were in intimate relationship with the extensor hallucis and with the peroneal aponeurosis. In the *Phoca* origin was from the craniolateral head of the tibia. In both the tendon passed over the middle of the instep and split into four branches, which extended to the four lateral digits. Murie reported no tibial origin for *Eumetopias* and *Odobenus*.

Stretching from the head of the fibula to the most prominent part of the external malleolus of *Zalophus* there was a sort of ligament, here termed the peroneal ligament. It is a development of the usual involved aponeurosis of the peronei, and in addition had connection with the aponeurosis of insertion of the hamstring muscles. Such an aponeurosis was present in the *Phoca* as well, but no definite ligament was encountered nor was direct involvement with the hamstring aponeurosis noted, possibly because of the more tender state of the tissue in the latter.

M. peroneus longus (figs. 12, 25, 26) arose from the lateral epicondyle of the femur. In the *Zalophus* it passed beneath the peroneal ligament and over a groove immediately caudad of the most prominent

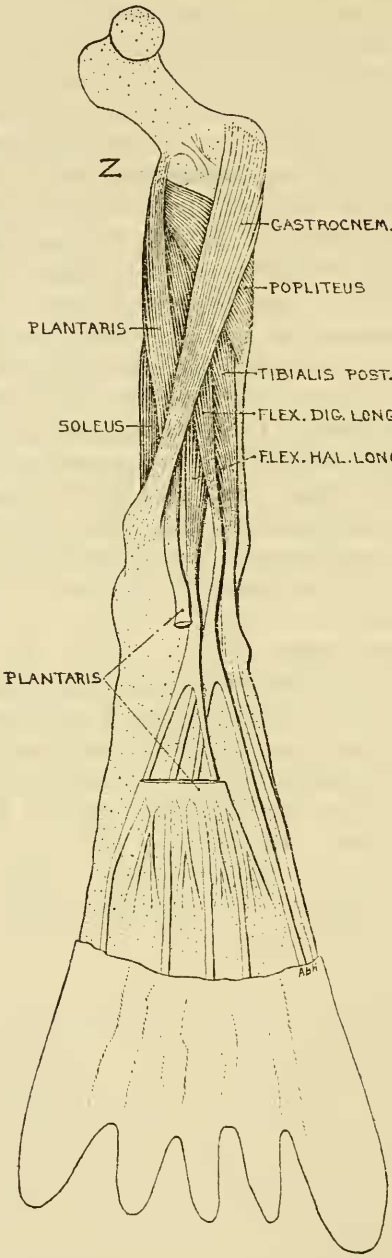

FIG. 27.—CAUDAL ASPECT OF THE MUSCULATURE OF THE LEFT POSTERIOR LIMB OF ZALOPHUS

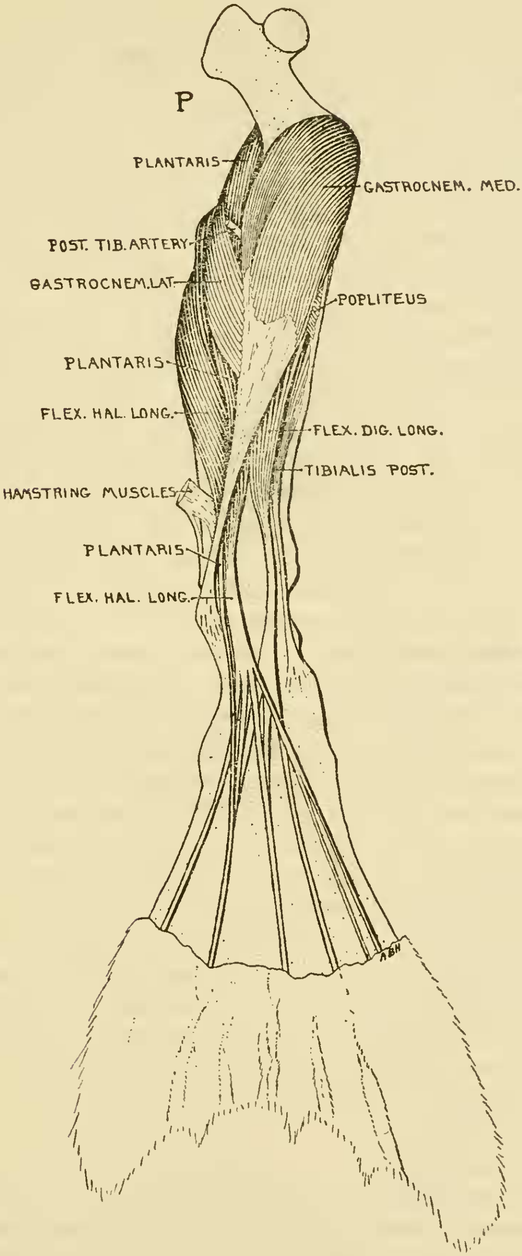

FIG. 28.—CAUDAL ASPECT OF THE MUSCULATURE OF THE LEFT POSTERIOR LIMB OF PHOCA HISPIDA

part of the external malleolus, over another groove upon the lateral calcaneum, to the plantar surface over the peroneal groove of the cuboid, and to an insertion upon the ventro-latero-proximal part of the first metatarsal. In the *Phoca* the tendon passed over a groove just craniad of the external malleolus, through the deep groove upon the lateral calcaneum, and then to the plantar surface through the peroneal groove of the cuboid, here so deep that it formed a bony tunnel arched over by a process of the cuboid in contact with metatarsal 5. There was also a groove for this tendon upon the first tarsale and insertion was normal upon the base of metatarsus 1. Miller considered that some of the fibers of this muscle took origin also from the tibia and fibula.

M. peroneus brevis (figs. 13, 25, 26). For a description of this muscle in the *Zalophus*, see the next. In the *Phoca* it was practically hidden by the peroneus digiti quinti. It arose from the proximal half of the cranio-lateral shaft of the fibula. Its tendon was in contact with that of the digiti quinti to distad of the calcaneum, at which point it diverged to insert upon the process directed ventrad upon the base of metatarsus 5. This has been reported as a separate muscle in the remainder of the eared seals that have been dissected, in *Arctocephalus* and *Eumetopias* arising deep to the digiti quinti and inserting upon the fifth metatarsal.

M. peroneus digiti quinti (figs. 13, 25, 26) in the *Zalophus* certainly occurred fused with the brevis division. This arose from the lateral head of the fibula and from half the lateral border of the shaft, from the peroneal ligament and from the deep aponeurosis of the soleus. The tendon passed over the lateral malleolus just caudad of the peroneus longus tendon, then beneath the latter, and over the peroneal groove upon the calcaneum, splitting into two branches, one going to the proximal termination of the first phalanx of digit 5 and the other to the metatarsal of the same digit. In the *Phoca* it arose by aponeurosis from the cranio-lateral head of the fibula. Its very slender tendon passed over the deep fibular groove directly caudad of the lateral malleolus, as in *Zalophus*. It then stretched distad along the lateral side of digit 5 as a well-defined tendon only as far as the basal phalanx. Miller said that in *Arctocephalus* it arose below the soleus, but this does not conform to his description of the latter muscle.

In *Odobenus* Murie found a peroneous quartus, and what he considered as the homologue of a peroneus tertius, the interpretation of the latter especially being doubtful, as it arose from the calcaneum. Its tendon joined that of the quartus division, and both therefore extended to the fourth metatarsal.

As with the manus, the short muscles of the pes are here omitted, the full account by Murie and Muller being deemed entirely adequate.

MUSCLE DIFFERENCES

Before the discussion of the functional differences between the Otariidae and Phocidae is undertaken it will be necessary to digest the more significant of the muscle differences and to tabulate them in condensed form, so that the variations may the more easily be grasped. Certain of the myological differences between the animals dissected are of such a character that it is difficult to compare them in words, especially concisely. Many of the muscles showing slight differences or of a character which are deemed relatively unimportant are omitted from the table and from the discussion. It is desirable to match muscular conditions of the Pinnipedia with one of the fissipeds, and solely because the domestic cat is far better known than any other this is selected for the purpose, and the nomenclature of its muscles reduced to terms comparable to those used for the pinnipeds. In the following table, then, those muscles are listed which have been found to differ in their origins or insertions, and the conditions in the cat (C) are given, followed by those in *Zalophus* (Z) and the *Phoca* (P).

Muscle	Origin	Insertion
Sternomast	C manubrium	lat. ½ occip. crest.
	Z presternum and craniad	lat. ⅓ occip. crest.
	P lat. presternum	mastoid proc.
Sterno-hyoid-thyroid	C 1st cost. cartilage	norm.
	Z manubrium deep to presternum.	norm.
	P 1st cost. cartilage	norm.
Scalenus ant	C ribs 2, 3	
Scalenus med	C ribs 3, 4	transv. proc. all cerv. vert.
Scalenus post	C ribs 6, 7, 8, 9	
Scalenus 1	Z rib 3	4th cerv. vert.
Scalenus 2	Z rib 1	5th cerv. vert.
Scalenus 1	P ribs 3, 4, 5	3d cerv. vert.
Scalenus 2	P rib 1	4, 5, 6th cerv. vert.
Scalenus 3	P rib 1	3, 4, 5, 6th cerv. vert.
Longus colli	C 2 norm. slips	norm.
	P 2 norm. slips	norm.
	Z 2 norm. slips, 1 complex atlantic.	
rect. cap. ant. maj	C cerv. vert. 2–6	norm.
	Z cerv. vert. 1–5	norm.
	P cerv. vert. 3–6	norm.
Panniculus carn	C carnivore type	
	Z modified carnivore type	
	P specialized type	
Pectoralis antibrach.	C manubrium	elbow.

Muscle	Origin	Insertion
Pectoralis maj. superfic.	C. cranial ½ manubrium	mid. ⅓ humerus.
Pectoralis maj. prof.	C manub. and sternebrae 1, 2, 3.	great. tuber. to ¾ humerus.
Pectoralis minor	C 6 sternebrae	prox. ½ humerus.
Pectoralis abdom	C xiphoid	to latis. dorsi and pect. minor.
Pectoralis superfic. ant.	Z presternal tip to rib 5	to wrist.
Pectoralis superfic. post.	Z rib 6 to xiphoid	great tuber. to manus.
Pectoralis prof	Z prestern. tip to xiphoid	1 delt. crest and to forearm.
Pectoralis	P dorsad prestern. tip to xiphoid and laterocaudad to near knee.	2 delt. crest.
Serratus mag	C ribs 1–9 or 10	norm.
	Z ribs 2–10	norm.
	P ribs 3–12	norm.
Depressor scapulae	C cerv. vert. 3–7	norm.
	Z cerv. vert. 3–7, ribs 1–4	norm.
	P cerv. vert. 3–7, ribs 1–2	norm.
Rectus abdominis	C norm	cost cart. 1, 2 and sternum.
	Z norm	cost. cart. 8, 7, 6, 5, not sternum.
	P norm	to sternum craniad to rib 1.
Quadratus lumborum.	C last 2 thorac. and all lumbar vert.	ilium.
	Z last 3 thorac. and all lumbar vert.	ilium.
	P last 2 thorac. and all lumbar vert.	sacrum.
Cephalohumeral	C from brachialis muscle	med. ½ occip. crest.
	Z prestern. tip; deep pect; delt. crest.	med. ⅔ occip. crest.
	P gt. and lesser tubers	sagittal crest.
Humerotrapezius	C middorsad axis to 4th thorac.	dist. ½ scap. spine.
	Z about middorsad axis to 4th thorac.	delt. crest and supinator longus.
	P about middorsad axis to 4th thorac.	scap. spine and delt. crest.
Spinotrapezius	C all thoracic vert. spines	2nd ¼ of scap. spine.
	Z caudal ⅔ thoracic vert	prox. ⅗ of scap. spine.
	P caudal ⅔ thoracic vert	prox. ⅓ scap. spine.
Rhomboideus dorsi	C middle cerv. to 4th thoracic.	vert. border scap.
Rhomboideus ant	Z med. ⅓ occip. crest	prox. ⅗ scap. spine.
	P nuchal ligament	glenovert. angle scap.
Rhomboideus dorsi	Z middorsum	vertebral border scap.
	P middorsum	glenovert. angle scap.
Atlantoscap. super	C absent	
	Z atlas	vert. bord. scap. craniad of spine.
	P atlas	vert, bord. scap. dorsad of spine.

Muscle	Origin	Insertion
Atlantoscap. infer.	C atlas and basioccip. Z atlas P atlas	metacromion. dist. ⅔ scap. spine. gt. tuber. and delt. crest humerus.
Splenius	C nuchal ligament Z nuchal ligament P nuchal ligament	entire occipital crest. entire occipital crest. mastoid process.
Trachelomastoid	C cerv. vert. 4–7 Z cerv. vert. 4–7 and thoracics 1–2. P cerv. vert. 3–7	mastoid process. mastoid process. mastoid process.
Biventer cervicis	C 7th cerv. to 5th thoracic vert. Z 5th cerv. to 4th thoracic vert. P 2nd cerv. to 2nd thoracic vert.	med. occipital crest. vertex. med. ⅓ occipital crest.
Complexus	C 3rd cerv. to 3rd thoracic vert. Z 2nd cerv. to 6th thoracic vert. P included with biventer cervicis.	med. ⅓ occipital crest. lat. occipital crest.
Rect. cap. post. maj.	C axis Z axis and 3rd cervical P axis	occipital. occipital. occipital.
Deltoid	C middle ⅓ scapular spine. Z entire spine and caud. vert. border. P entire spine	deltoid crest. deltoid crest and supinator longus. deltoid crest.
Teres minor	C prox. glenoid border of scapula. Z lat. scapula, broadly P lat. scapula, narrowly	gt. tuber. of humerus. fused with infraspinatus. fused with deltoid.
Teres major	C prox. ⅓ glenoid border of scapula. Z prox. ⅓ glenoid border of subscapularis. P axillary ½ infraspinous space.	3rd tenth of humerus. middle of humerus. proximad middle of humerus.
Episubscapularis Subscapulo-capsularis.	Z present in *Zalophus* only P present in *Phoca* only	
Brachialis	C distal ¾ humerus Z prox. ⅔ humerus P prox. ⅔ humerus	norm. norm. norm.
Triceps long	C dist. ⅓ axillary border scap. Z infraspin. ridge and onto vert. border. P dorsal ⅓ infaspin. ridge and onto vert. border.	olecranon. forearm fascia. forearm fascia.

Muscle	Origin	Insertion
Triceps lat	C deltoid ridge Z humeral neck P delt. crest and distal scapula.	olecranon. forearm fascia. olecranon.
Triceps med	C prox. 1/5 humerus Z entire humeral shaft P entire humeral shaft	olecranon. olecranon. olecranon.
Anconeus internus	found in the pinnipeds only	
Palmaris longus	C entepicondyle Z entire medial face ulna, huge. P olecranon	norm. norm. norm.
Flex. digit. communis 1. Flex. digit. communis 2. Flex. digit. communis 1. Flex. digit. communis 2. Flex. digit. communis 3. Flex. digit. communis 4. Flex. digit. communis 1. Flex. digit. communis 2. Flex. digit. communis 3.	C from palmaris long. and flex. profundus. C entire ulna; entepic; middle 1/3 radius. Z 4th tenth of ulna Z entepicondyle Z middle 3/5 radius Z entepicondyle P entepicondyle P prox. 2/3 ulna P 3rd eighth of radius	4 lat. digits. 5 digits. digits 3, 4, 5. digits 4. digits 1, 2, 3. digit 1. 5 digits.
Flex. carpi ulnaris	C entepic. and olecranon Z olecranon P olecranon	pisiform. pisiform. pisiform and metacarp. 5.
Abduct. dig. 5 longus.	P in *Phoca* only, from olecranon.	digit 5.
Supinator longus	C middle 1/5 humerus Z prox. 2/3 humerus, broadly P prox. 1/3 humerus, narrowly.	distal radius. distal radius. distal radius.
Psoas minor	C last 2 thorac. and 1–3 or 4 lumbar vert. Z last 3 lumbar P last 3 lumbar	ilio-pectineal line on innominate. ilio-pectineal process. ilio-pectineal process.
Psoas magnus	C last 2 thorac.—7th lumbar Z last 2 lumbars and sacrum P last thorac., all lumbars, and sacrum.	lesser trochanter. lesser trochanter. med. tuberos. of tibia.
Iliacus	C ventral ilium Z ventral ilium P ventral ilium	lesser trochanter. lesser trochanter. medial tuber. tibia.
Gluteus quartus	Z present in *Zalophus* only—weak.	

Muscle	Origin	Insertion
Quadratus femoris	C ischium Z ischium P absent	distal greater to lesser troch. whole femoral shaft.
Semimembranosus	C ischial tuber Z caudo-ventral ischium P caudo-ventral ischium	entepicond. femur and prox. tibia. 4th fifth of tibia. 2nd to 4th fifth of tibia.
Semitendinosus	C ischial tuber Z spines 3d–6th caudals P {transv. proc. 1–3 caudals, caudal ischium}	2nd fifth of tibia. distal ¼ tibial shaft. 3d and 4th fifths of tibia.
Biceps femoris	C ischial tuber Z {spines 2–7 caudals, transv. plate 2nd sacral} P {dorsal ischial spine, transv. plate 3d sacral}	prox. ⅓ tibia, and patella. femoral condyle to distal shank. prox. ⅞ of shank.
Sartorius	C crest and vent. border ilium. Z {ventral angle ilium, ventral angle ilium} P ventral angle ilium	prox. ¼ tibia, and patella. patella. medial tuberos. tibia. patella.
Vastus lateralis	C gt. trochanter and prox. ⅖ femur shaft. Z gt. trochanter and prox. ⅖ femur shaft. P gt. trochanter.	patella. patella. patella.
Vastus profundus	single in pinnipeds; double in cat.	
Pectineus	C cranial pubis. Z pectineo-psoal process P cranial pubis	distal base lesser troch. distal base lesser troch. distal base lesser troch.
Gracilis	C symphysis pubis Z position comparable to symphysis. P position comparable to symphysis.	3d sixth of tibia. medial third of tibia. distal ⅓ of tibia.
Adductor 1 Adductor 2 Adductor 1 Adductor 2 and 3 Adductor 4 Adductor 5 Adductor 6 Adductor 1 Adductor 2	C caudal ramus ischium C cranial pubis Z caudal ischium Z caudal ½ pubis Z medial pubis Z cranial pubis Z cranial pubis deep to 5 P cranial pubis P caudal ½ pubis	whole shaft femur. 2d and 3d fifth of femur. med. tuber. tibia and epicond. femur. dist. gt. troch. to entepicond. 2d fifth of femur. entepicond. of femur. lesser troch. middle ⅗ of femur. base gt. troch.
Gastrocnemius lat	C large Z absent P small	norm. norm. norm.

Muscle	Origin	Insertion
Plantaris	C tendon over caudal calcaneum. Z tendon over medial calcaneum. P tendon over medial calcaneum.	
Soleus	present in the cat and *Phoca* only.	
Flex. digit. longus	C middle ½ tibia Z fibular head P fibular and tibial heads	to tendo flex. hallucis longus. digits 1, 3, 4. digits 2, 3, 4.
Flex. hallucis long	C middle $^5/_7$ of tibia Z prox. ⅔ interos. membrane. P prox. ⅔ fibula	tendons to all digits. digits 2, 5. digits 1, 3, 4, 5.
Tibialis posticus	C prox. ⅓ tibia Z fibular head and prox. ¾ tibia. P prox. ⅗ tibia	norm. norm. norm.
Extens. digit. longus	C ectepicond. femur Z ectepicond.; tibial head; prox. ⅔ fibula. P tibial head	4 lat. digits. 4 lat. digits. 4 lat. digits.
Peroneus longus	C prox. ½ fibula Z ectepicond. femur P ectepicond. femur	all 5 metatarsals. metatar. 1. metatar. 1.
Peroneus brevis	C distal ½ fibula Z fused with next P prox. ½ fibula	metatarsal 5. metatarsal 5. metatarsal 5.
Peroneus digiti 5	C absent Z with last, prox. ½ fibula P fibular head	 digit 5. digit 5.

When one casually examines either a dissection of the animal itself or of a series of drawings of a pinniped he will likely be struck by the apparent vastness of the difference from what may be termed a normal mammal, but this difference is not as great as it seems, and a detailed study, muscle by muscle, will lead the investigator to the opposite extreme and mildly astonish him that a mammal which departs in many details so widely from the generalized type can adhere so faithfully to the fundamental carnivore plan of myological arrangement. The pinniped osteology is, of course, very specialized, and the muscle attachments must synchronize accordingly, which is the main reason why the musculature appears so complicated at first sight.

In the above table the origins of the *Zalophus* resemble those of the *Phoca* in a few more instances than they differ, while the differ-

ences of insertion outnumber the resemblances. The muscles above listed, both in origin and insertion, differ from those of the cat in about 14 per cent more instances in *Zalophus* than in the *Phoca*, but the differences in origin are more numerous than those of insertion. On the other hand, when these muscles of *Zalophus* are compared with those of the *Phoca* it is found that the origins are more conservative, while the insertions are more prone to differ.

Little or no account can be taken of muscles which may be relatively more or less robust because of the difficulty of comparing the cat, the lean otariid, and the fat phocid. The following comparisons may, however, be made, with the cat as standard:

Muscle conspicuously broader at origin: Pectoralis in both, and biceps femoris in *Zalophus*.

Body muscles that are shorter: In both genera the sternomastoid and scalenus, the latter in *Phoca* especially.

Occipital muscles with broader attachment: Cephalohumeral in *Zalophus*.

Occipital muscles with narrower attachment: Cephalohumeral and splenius in *Phoca;* biventer cervicis in *Zalophus;* and sternomastoid in both, especially the *Phoca*.

Limb muscles whose origins have shifted distad: Triceps medialis, palmaris longus, flexores carpi ulnaris and hallucis longus, and extensor digitorum longus pedis in both animals.

Limb muscles whose origins have shifted proximad: Brachialis, triceps longus, flexor digitorum longus pedis, and peronei longus and brevis, in both animals.

Limb muscles whose insertions have shifted distad: Pectoralis (part), humerotrapezius (especially in *Zalophus*), teres major, triceps longus, semimembranosus, semitendinosus, and biceps femoris, in both; deltoid, triceps lateralis, quadratus femoris, and adductores 1, 2, 3, and 5 in *Zalophus;* and atlantsocapularis inferior, psoas magnus, iliacus, and gracilis in the *Phoca*.

The inclusion or ommission of some muscles in the above groupings are at times largely arbitrary, for it may be difficult to be sure whether a muscle is attached only to the tibial head, for instance, or whether it also encroaches upon the femoral condyle. Also it must be taken into account that most of the limb muscles are relatively shorter than those of the cat usually merely for the reason that the bones themselves are shorter.

It is to be seen that only two of the body muscles of the Pinnipedia listed in the tables (pp. 101 to 106) have become shorter, and these to a very slight extent. One muscle of the occipital crest has become broader and four others of this region narrower in their attachment. The origins of five limb muscles have shifted distad and five others proximad, to a very slight extent in all cases save

that of the triceps, and 14 of the insertions of *Zalophus* and 11 of *Phoca* have shifted distad. Further scrutiny shows that almost all of these insertions that have shifted distad are muscles of the upper arm and thigh, while of the antibrachial and shank muscles whose origins have shifted half have moved proximad and half distad, an exception being the triceps longus. On the average, therefore, the tendency has been toward a lengthening of the limb muscles, not actually but in respect to the positions of their bony attachments.

DISCUSSION

In the following pages *Zalophus* and *Phoca* will be discussed as two mammals that are chiefly aquatic, differing from each other in certain respects and from the normal terrestrial carnivore in others. There will be no discussion in the present paper of the probable derivation and but little regarding the relationship of the Otariidae and Phocidae, nor of certain broad principles and laws intimately correlated with the development of a mammal for an aquatic life. It may be mentioned, however, that the writer considers the serious comparison of the otariids with the bears and of the phocids with the otter (as Mivart, 1885), in an attempt to prove that the ancestry of these two pinniped families can be traced to members of groups now living, to be a rather unprofitable pastime. There are many resemblances, it is true, but it is very probable that the eared seal phylum is older than the bears. Not only is the Pinnipedia a very ancient order but the carnivore stem has had very numerous branches, and it is extremely unlikely that the protopinniped was at all like any living fissiped.

In all the pinnipeds the relaxed position of the anterior nares is almost closed and naturally remains so between respirations even when the animal is on land, although I have seen a sea lion maintain its nostrils in a dilated position for several minutes at a time, and also a phocid when panting after considerable exertion. Tight closure can be effected both by contraction of the naso-labialis, pulling the mystacial pad against the nostril, and by contraction of the fibers of the mystacial pad itself, which radiate toward the surface and probably have some voluntary muscle action. Expansion of the nasal opening is effected by flexion of the maxillo-naso-labialis, which pulls the mysticial pad laterad. This pad is much broader and thicker in the phocid, but there was apparently no difference in the operating mechanism of the anterior nares to account for it. Possibly the reason for the difference in size of the pads may be found in some variation of the tactile function of the vibrissae. In breathing on land the otariid keeps the nostrils virtually closed between breaths, opens them moderately at exhalation and widely during inhalation.

In the water this animal often swims partly on its side and when coming to the surface for breath, will inhale through the corner of the mouth as well as through the nose, as a human swimmer often does. Perhaps more frequently, however, it will break water with the tip of the nose and breathe through this member only, as the phocid usually, if not always, does. It may be mentioned in this connection that the epiglottis of *Zalophus* appears to be unusually small for the size of the animal, which one would not expect to be the case in an aquatic form which habitually comes to the surface for quick breaths.

I have encountered no statements regarding the possible duration of submergence of the Pinnipedia which I regard as both significant and trustworthy. In captivity an animal seldom experiences any incentive for lengthy submergence and I have never seen one do so for more than about two minutes. If frightened in the wild, the animal which reappears can not always with confidence be regarded as the same one which has disappeared. It seems certain that all pinnipeds must be able to stay beneath the surface for some considerable time, while it would seem absolutely essential that the boreal members of the Phocidae, at least, which must often have to swim beneath extensive ice floes, should have this faculty especially developed. Of undoubted importance in the present connection is the development in this order of a large hepatic sinus, consisting of a remarkable dilation of the vena cava dorsad of the liver. For the Phocidae this was said by Murie (1874, p. 545) to have been reported and illustrated by Barkow (presumably H. C. L. Barkow in the early nineteenth century), but I have been unable to find the article to which he refers. Murie (1874) states that in his *Eumetopias* the sinus occupied " a volume, one might almost say, greater than the glandular hepatic organ itself." In examining the viscera of the *Phoca hispida* which I dissected, Paul B. Johnson encountered such a sinus, dilatable to contain perhaps 2 quarts, but in the younger *Zalophus* it was much less developed. It is, therefore, possible that this sinus is developed with age and that it is largely lacking in juveniles. It is, of course, apparent that it serves as a reservoir to hold an extra amount of blood and hence to prolong submergence by just so much. Throughout sealing literature one often encounters statements to the effect that pinnipeds appear to be veritable sacks of blood.

While on the subject of the viscera it may be well to mention, in passing, the habit of the Pinnipedia of swallowing stones, sometimes as large as an egg and aggregating as much as 3 pounds in weight. The reason for this action has not been determined.

In the *Zalophus* the ear is slender and had a length of 28 mm. The external opening of the auditory tube is small and the pinna of

the ear laps at the base, so that when the ear is pulled backward by the cervico-auricular musculature, flexion of the mandibulo-auricular complex furls the base of the pinna and effects complete closure of the tube. There is no conspicuous valve within the tube. In *Phoca hispida* conditions are considerably different, for there is no external ear or pinna. Near the orifice, however, there is a small fibrous plug which acts as a valve to close the tube upon contraction of the mandibulo-auricular. No action of the cervico-auricular muscles could be detected in living animals. Dissections of Ernst Huber, however, indicate that there is considerable specific variation in the mechanism for closing the ear of the Phocidae.

The auditory tube is not longer in the phocid, and so the external auditory orifice is really no farther dorsad in this animal than in the otariid, but the sagittal line is higher in the latter, and this increases with age, so that in reality the top of the head is higher above the ear and the head must be thrust higher out of water for the animal to hear. In the phocid the eyes also are directed more dorsad (15° to the vertical as against 50° in the otariid), and the external nares as well (45° to the cranial axis as against about 20° in *Zalophus*), so that eyes, ears, and nostrils are so placed in the earless seal that these organs of sense may be utilized while the animal exposes the minimum amount of its head above the surface of the water—a definite aquatic modification developed to a greater degree than is the case in *Zalophus*.

Quite diverse stimuli seem to have been instrumental in molding the characteristics of the neck in the otariid and the phocid. In adult bulls of the former the neck acts partially as a repository for surplus fat accumulated to sustain the animal during the breeding season. Unfortunately proof is at present impossible, but I am strongly of the opinion that at the approach of the breeding season when the otariid bulls must do battle for the females, the increase in the swelling of the neck is also partially due to an enlargement and coarsening of certain of the cervical muscles, this action being caused by a hormone or similar secretion of the awakening sex glands. This had puzzled me for some time until O. J. Murie informed me that he had noted a great increase in size of certain neck muscles (chiefly the sternomastoid I believe) during the rutting season of the caribou (*Rangifer*), the purpose of which is evidently to add to the fighting ability of the bulls. This is entirely comparable to the relatively great increase in the length and size of some of the perineal muscles of female mammals at the imminent approach of parturition.

This cervical swelling does not take place in females and young bulls of the Otariidae. Even in old bulls submersion lightens the weight of the neck, and the more powerful musculature of this sex may theoretically handle the large neck even more agilely under

water than is the case with females and young males. At any rate, even though the neck is relatively no longer than in the cat, it always has the appearance of being long and flexible, capable of great contortion and great precision of movement. This has been developed in the pursuit of agile prey, necessitating darting movements of the head here and there, and also in the sinuous movements which this family is seen to use while swimming, thrusting the head this way and that as an accessory rudder in aid of the more posterior one (the hind feet), with the middle thorax as the fulcrum of leverage. For the reason that natation is almost exclusively by means of the fore feet, this sinuous development of the neck has not been inhibited by a more powerful stimulus, as seen to best advantage in Cetacea and to a lesser extent in the Phocidae, in both of which the neck acts as part of the fulcrum upon which acts the lever of the posterior end of the animal during swimming. The mobility of the head and neck of the otariid is further increased by the part which they play in terrestrial locomotion, during which the neck violently sways back and forth, not only to maintain proper balance, but as a direct aid, chiefly through the broadened cepahlohumeral, to rhythmic motions of the forelimbs. Besides the cephalohumeral, other broad muscles which aid in diverse movements of the head are the anterior rhomboid, splenius continuous with the trachelomastoid, and the broadened insertion of the sternomastoid; and the exceedingly complex third or atlantic division of the longus colli must also have an important bearing in this connection.

There is apparently no reason why an agile neck would not be of great advantage to a *Phoca* also, and it is not meant to imply that this member is actually stiff. But the fact remains that extensive observation of both sea lions and seals shows that the latter uses its neck in a different manner. It seems actually to have extensibility and may be stretched to a surprising degree, but in retrieving a dead fish there is not the speedy action and "catch on the fly" of the otariid, but a more deliberate nuzzling and capture, nor is the head and neck moved much as an aid to terrestrial progression. The articulations of the vertebrae are doubtless as free, but the muscles are apparently used in a different manner. Largely instrumental in this lack of agility is the fact that in this family, as in the Cetacea, practically all the motive impetus during aquatic progression is furnished by the extreme posterior end of the animal, and the neck as well as the anterior thorax acts as the fulcrum upon which works the powerful musculature of the lower back. The head, together with the forefeet, doubtless plays a most important part as a rudder, but in very circumscribed movements, for a slight twist dorsad or laterad would be all that was necessary. In other words, no animal that

propels itself through the water at speed by means of its posterior parts can wave its head around in all directions, but an otariid, with center of motion near the middle of its mass, can move the head in any direction it pleases if it at the same time employ its rear end in antagonistic or compensating movements.

Accompanying this state of affairs is found a distinctive condition of the muscles with attachment to the occipital crest and ventrad. In contrast to the situation in *Zalophus*, in the *Phoca* the cranial attachments of the cephalohumeral, humerotrapezius, and anterior rhomboid are narrowly confined to the vicinity of the vertex, while the middle and ventral parts of the occipital crest are free of all muscles which are more characteristic of the normal occipital crest, the superior oblique being the only one found here. As the above have narrowed mediad, so the others have narrowed ventrad, and the insertions of the sternomastoid, trachelomastoid, and splenius are confined to the mastoid process. Thus the muscles here discussed are better situated to work in two planes of movement in the *Phoca*—directly dorsad and directly laterad—which are most effective in rudder movements, rather than muscles fitted for movement in all directions, as in the otariid.

The number of vertebrae in the thoracico-lumbar series, 20, is the same as in the majority of fissipeds, which is one more than the primitive number as mentioned by Todd (1922), while the tendency in most orders is toward an increase in the number of this series. The almost total lack of definition of the neural spines in the anterior thoracic region of *Phoca* conforms to the claim by Harrison Allen (1888) that these spines are practically absent in those mammals which do not use the anterior limbs for support, such as *Dipus* and the bats. This statement furnishes food for thought, but the conditions are far from being as simple as implied, for in the Cetacea, which have surely abandoned manual support for a longer time than any other mammal, the neural spines of the anterior thorax are always well developed and at times are enormous. It might be thought that in view of the greater development of the back muscles in the Phocidae the spines might be higher than in the Otariidae, rather than so much lower, but such is not the case, and it is probable that the narrow, deeper back musculature of *Zalophus*, with the longer spines, has developed for movements of all sorts, especially in the sagittal plane, while the immensely broad back musculature of *Phoca*, with wide vertebral articulations and very low spines is in response to movements that have been so largely lateral. Photographs of *Mirounga* (see fig. 29) show that from a prone position on land this animal can elevate the anterior part of the body, including most of the thorax, to an absolutely vertical position in a manner that one would judge to be beyond the power of any mammal. There

is no skeleton of this genus at hand but I can not find any modifications in other Phocidae examined that might permit such an unusual position to be assumed.

No very significant differences in the thorax proper can be detected, save a tendency toward broadening in the phocid and apparently the lengthening in the otariid, possibly due in the latter to the advantage of having bony protection against hydrostatic pressure over the greatest possible area of the abdomen. The presternum that is well developed in both animals has undoubtedly been lengthened by a forward extension of the pectoralis, which is of such prime importance to the swimming of the otariid, and probably secondarily so in the phocid.

In the present paper there will be no attempt to calculate by formulae the leverage and potential strength of the limb segments and their muscles. Such treatment of the subject gives the result a profound and scholarly appearance, but the writer views with the greatest distrust all such treatments, for they can not take into consideration the differences of fascial attachment, and no one can tell exactly what any particular muscle either can or will do.

The anterior limb of the Pinnipedia as it now occurs is the result of three stimili which are hard to unravel—the fact that the proximal part is within the body, operative in both; phylogenetic influences, of an unknown degree of resemblance; and the fact that the forelimb is the primary organ of propulsion in the Otariidae and practically inoperative for this function in the Phocidae. In the otariid the foreflipper is one of the most important, and in the phocid, one of the least important, parts of the body. On land the former animal uses this member as normally as its proportions will allow. It is extended at the wrist at a right angle to the antibrachium, the toes being directed almost directly laterad. In the latter the manus may be used to help the animal from the water or over a rough spot, but its shortness and the thick blubber layer often present over the chest raise the manus too far from the ground for it to be of great use. Hence it is usually held somewhat pendant and abducted (from the forearm). As far as I can tell the most natural, static position of the anterior limb in both animals is with the humerus at slightly less than 90° to the scapular spine. In the otariid the antibrachium is almost extended, and in the phocid flexed to almost 90°. In the former the manus is almost on a line with the antibrachial axis, and in the latter, abducted to at least 45°—usually more. The static posture of these segments with relation to each other is shown in Figure 30.

In the water the otariid moves with broad sweeps of the powerful manus, recovery being made with the radial border of the arm pre-

sented craniad, while the rear limbs play a very minor part as far as I have observed, never being used in rhythmic motions, but in various steering movements. During brisk swimming the forefeet of the Phocidae are folded against the body save when the animal wishes to make a sharp turn, at which time the outside flipper will be abducted and thrust against the water, as a man would push against a wall in making a similar movement. When a seal is merely loafing about in the water, with slight turns, rolls and such idle actions without definite idea of progression, the hind limbs may be entirely immobile while the forefeet maintain an intermittent "fiddling" movement, such as a man would employ while treading water. I have no doubt that when the seal is suddenly alarmed it employs its forelimbs in active swimming movements in any way which might be of assistance in starting quickly.

It is almost impossible to determine the degree of pronation and supination of which the whole arm is capable, for so much of it is within the body covering that in the entire animal one can not follow the interaction of the joints, and after sufficient of the muscles have been cut away to determine this the results are worthless because many of the inhibitions to movement normally raised by taut muscles and bulk of tissue have been removed. It is probable, however, that at least in *Zalophus* there is less of such movement possible than in man, while in both there is more than in such a fissiped as the cat.

Few conclusions regarding the scapula may be reached, and its chief stimulus for specialization in the Pinnipedia is doubtless as a scaffold upon which are hung the arm muscles, rather than as an attachment for muscles of the thorax and neck. It is relatively more robust in the *Zalophus*, as one would expect, but contrary to expectations, the axillary border is relatively the longer in the *Phoca;* for this animal has less need for a long lever arm for the triceps. In the Otariidae at least the scapula is unusually mobile, and slides about beneath the skin when the animal is in terrestrial movement in exaggerated manner. When resting with head low the scapulae may be in contact, projecting for several centimeters above the dorsal line, or by means of the serratus magnus and depressor scapulae muscles they may be forced well ventrad, which correspondingly lifts the body. Incidentally it may be mentioned that in most of the articulated skeletons which one sees the thorax is elevated above the ground to an unnatural extent.

In the *Zalophus* the supraspinatus is large and powerful as an aid to extension of the humerus but in the *Phoca* [5] it is considerably weaker, as one would also expect. In both animals the infraspinatus

[5] At least in *Mirounga*, among the Phocidae, the supraspinous fossa is relatively quite as large as in the Otariidae.

(a rotator) is very weak while other muscles have encroached upon the infraspinous space of the scapula, which is especially the case in the phocid, for here this space is relatively considerably larger than the supraspinous fossa. There is no very clear reason to be seen for the extension caudad of the glenovertebral cartilage of the *Phoca*, although it is self-evident that it has taken this course in response to stimuli supplied by the muscles attached thereto.

The percentage of arm length (humerus, radius and manus), based on the bones only, to body length is in a cat skeleton 82, *Zalophus* 66, and *Phoca* 48 per cent, so it is seen that in comparison with a fissiped the phocid arm is much reduced, while that of the otariid occupies an intermediate position. In the same order as above, the length of the humerus compared to body length is, respectively, 31, 18, and 14 per cent; of the radius, 30, 20, and 14 per cent; and of the bony part of the manus, 21, 29, and 20 per cent. It is thus seen that there has been a shortening of the two upper segments of the pinniped arm and that the proportions of one segment to the other have remained almost the same as in the fissiped, save possibly that the rate of reduction in the size of the humerus has been a bit more rapid in the case of *Zalophus*. There has been no change in the size of the manus of *Phoca* relative to the entire arm, but that of the *Zalophus* has increased in relative size (compared to the more proximal segments) about one-third. Presumably, however, this osteological increase in the size of the otariid manus has not been sufficiently rapid to meet the needs of the animal and a still larger area for furnishing propulsive force has been acquired by the development of cartilagenous extensions to the digits. As an alternative one must consider the unlikely possibility that the presence of these cartilages is due to some stimulus other than that caused by the need of a longer manus in swimming. At any rate, they have made the functional length of the manus (measured to its tip) of the *Zalophus* about 40 per cent of the body length, or, from a relative standpoint, fully twice as long as in the *Phoca*. From still another aspect, the effective length of the anterior limb operating against the water is the distance from the axilla to the tip of the flipper. In the *Zalophus* with the axilla at a point just proximad to the middle of the ulna, this amounts to 52 per cent of the trunk length. In the *Phoca*, the axilla is opposite the ulnare and the corresponding percentage is about 19. As the anterior limb is used for such very different purposes in the two families, however, a comparison of the visible portions does little but call attention to their dissimilarities.

In the Otariidae the extended arm may be operated to good advantage as a swimming organ by muscles coming from other parts of the body. Thus the cephalohumeral is attached in part to the

deltoid crest but it also has connection with the tissue about the presternum and the border of the pectoralis. Its chief action is upon the head and neck but it also extends the humerus both in swimming, and upon the land by means of lunging, forward and back movements of the head, and is thus of definite aid in terrestrial progression. It is also involved with action of the anterior part of the pectoralis, which by means of its insertion as far distad actually as the palmar tissue, adducts the arm with much power. Of the greatest importance in strong backward sweeps of the flipper are the intimately connected posterior portions of the pectoralis, the latissimus dorsi, and most of the panniculus carnosus, all of which have a long power arm upon the anterior extremity. In the *Phoca* these muscles perform other work and will be discussed elsewhere.

Relative to length of body the humerus of *Zalophus* is less than 65, and of the *Phoca* about 45 per cent of the length of this bone in the cat. It is proportionately massive, with prominent and broad processes and ridges. Both of these details denote great power of the muscles attached. The humeral head differs somewhat in the two animals, indicating that the normal position of the humerus in *Phoca* is slightly more flexed and abducted than in *Zalophus*. Extension and flexion of the humerus is limited largely by the fact that it is entirely within the body covering and that the integument limits the movements of the forearm also; but abduction of the humerus is fully as great as in many fissipeds—*Canis* for instance. As the arm is largely within the body, flexion of the part distad of the humerus, by the single biceps and brachialis, is limited, while extension of the humerus is well provided for by a complex triceps with a leverage much greater than in the normal fissiped.

In the otariid the great height and massiveness of the greater tuberosity is for supplying increased leverage to the large supraspinatus which helps extend the humerus—a motion of much importance in recovery after a backward sweep of the foreflipper. This movement is not of importance to the *Phoca*, so the supraspinatus is small and the greater tuberosity lower than the femoral head. The enormous development of the deltoid crest, extending distad from the greater tuberosity for two-thirds the distance to the condyle in *Zalophus* and half the distance in *Phoca*, is of the utmost importance in not only supplying several times the leverage to the shortened bone that these muscles could furnish to a humerus of the human type, but also, through the great elevation of the deltoid crest, in presenting an efficient lever arm for strong rotation, needed in the "feathering" action of the flipper of *Zalophus* in swimming. The cephalohumeral, humerotrapezius, and pectoralis have probably had far more to do with the elevation of this crest than the deltoideus. In the *Phoca* the deltoid crest, although not quite so long is fully as high—

higher distad. It can not play the same part in the economy of this animal as in the otariid, for the forelimb is practically useless as a swimming organ. Of course the high deltoid crest may be a relic from a time when the foreflipper may have been so used, but I believe another explanation is the proper one, and this is that the high deltoid crest of the *Phoca* was developed in response to stimuli provided by strong antagonistic action of the muscles attached thereto; in other words, that it has acted as a static fulcrum while the animal is swimming. The more caudal part of the pectoralis and the latissimus dorsi are both of decided aid in the rhythmic lateral swimming movements of the posterior body. These insert upon the deltoid crest, which is held static as a fulcrum by the atlantoscapularis inferior and humerotrapezius. It is not meant to imply that this has been the only stimulus, but it was probably the most important.

The lesser tuberosity of *Phoca* is enormously developed and is much higher than either the head or the greater tuberosity; but in *Zalophus* it is low, although very prominent. The condition in the phocid is not attributable to any complexity of muscles attached to this tuberosity, for almost the sole influence is the subscapularis. At least a part of the height of the process is due to the fact that in this animal the normal position of the humerus is a bit more abducted; but this seems insufficient to account in full for the condition and other logical reasons are obscure. The medial epicondyle, giving rise to a number of the forearm flexors, is larger than the lateral in *Zalophus*, as is the usual case in fissipeds, but both epicondyles are unusually massive. The flexors of this animal are, of course, of the utmost importance in operating the powerful backward sweeps of the flipper employed in swimming. In the *Phoca* the lateral epicondyle is fully as large as, if not actually larger than, the medial, and it is readily seen that in the phocid function of the arm while swimming, extension, in the way of brisk dorsal motions, is fully as important in steering movements as ventral ones. In consideration of the difference in the function of the forearm in the two animals it is rather unexpected to find precise similarity in the direction that the origins of the antibrachial muscles have migrated, which may be interpreted as evidence of some strength in favor of the uniphyletic origin of these two families of pinnipeds. This migration, as already mentioned, consists of a movement distad from the femur to the antibrachium of the palmaris longus, flexor carpi ulnaris (part), and flexor hallucis longus. In both animals there has been a movement distad of other muscle attachments which are characteristically of the humerus, but it is likely that this has been due to a more speedy rate of shortening for the *distal* than for the proximal part of the humerus.

It is quite remarkable that during the reduction in the size of the pinniped arm the relative proportions of the humerus and radius have remained virtually the same both in the *Zalophus* and the *Phoca*, as in the cat. There are two other measurements of this segment that are also worthy of mention—the length of the ulna and the width of the radius. In the cat the length of the ulna is 114, in the *Zalophus* 123, and in the *Phoca* 131 per cent of the radial length. This is not a great difference but the disparity is not in the expected direction. A great length of the olecranon is associated with strength of extension of the antibrachium, which one would expect to be an attribute of Zalophus—not a *Phoca* with its small, weaker manus. One can readily understand how an increased width of the antibrachial bones is correlative to the use of the forelimb as a swimming organ, this being an inevitable result of the turning of this limb into a broad, thin paddle. The Cetacea show this character to a strong degree and it is an expected characteristic of *Zalophus*, in which the greatest width of radius is 29 per cent of its length, but why this same proportion should be 35 per cent in the *Phoca* is unknown. Save for the deep grooves upon the distal part of the radius of *Phoca*. the other details of this bone mentioned in the osteological description are without any especial significance in the present connection. These grooves would be developed by agility rather than strength, and it is likely that they have been deepened by the same sort of "fiddling," water-treading movements of the flipper already mentioned, but there may be additional reasons for their appearance. There is no indication in the pinnipeds of any twisting of the shafts of the antibrachial bones, as so oftens occurs in fissipeds for the purpose of directing the manus straight craniad for increased facility in walking.

The proximal part of the ulna is of great depth, especially in *Zalophus*. This is due in this animal to the enormous width upon the medial face of the bone, of the head of the palmaris longus, arising from all this broadened portion, while in the *Phoca* this muscle is confined to the olecranol border, and the medial face of the ulna is occupied by a part of the origin of the flexor digitorum communis. Another muscle that has apparently acted to deepen the proximal part of the ulna of *Zalophus* is the extensor pollicis longus, occupying the ulnar two-thirds of the lateral face, while in the *Phoca* the origin of this muscle is very much narrower.

After transection of the antibrachial muscles it was found that through the forearm, chiefly the radius of course, the pronation-suspination movement of the wrist in respect to the humerus is about 40° or 45° in *Zalophus* and fully 80° in *Phoca*.

In *Zalophus* the manus continues from the antibrachium in almost a straight line, in static position the axis diverging from this by not more than 15°, with adduction almost zero and abduction to 45° (in the partially dissected specimen). In the *Phoca* the static position of the manus is at an abducted angle with the forearm of about 45°. Adduction from this position is almost entirely inhibited by the tension of the abductor digiti quinti—probably slightly more yielding in life—but maximum abduction is to an angle of 90° with the forearm. As already mentioned the proximal articular surfaces of the *Zalophus* scapholunar and ulnare, and of the metacarpals extend farther upon the dorsum of these bones than in the *Phoca*, but it was found that in the preserved animal the chief center of movement was at the articulations *distad* of the scapholunar and ulnare, due to the looseness of the capsular tissue at this point. Extension of the manus allows the metacarpals to be placed at a right angle to the forearm but no more, while almost the same amount of flexion is permitted. Provision is not made at the articular surfaces of the carpal bones of the *Phoca* for the same amount of extension, but this is nevertheless permitted by the looseness of connection of all the carpal bones. This same looseness allows flexion to the excessive point where the metacarpals are parallel with the bones of the forearm (after removal of the integument and fatty tissue). As there has been no twisting of the antibrachial bones the manus, in relaxed posture, presents its radial border almost directly craniad. Presumably this position is the best in both animals for the work which the manus has to perform, as it certainly is for terrestrial locomotion in *Zalophus*, disposing of the long tip of the manus in a way that will interfere the least with walking.

There seems to be little of functional significance in the carpus of *Zalophus*, as it is just the sort one would expect to find between the broad antibrachium and the metacarpus. There are several points about the carpus of *Phoca*, however, which attract attention. It is rather narrow proximad, which has probably been brought about by much movement of the manus in the plane of abduction-adduction. Abduction is very materially assisted by the peculiar abductor digiti quinti. As this has become more specialized it has pulled the manus more and more laterad until now its natural tone prevents adduction of this segment even as far as the antibrachial axis. Abduction to 90° is possible, however, as already mentioned, and this is correlated with a specialized, "mitred" condition of the carpus as a whole, suggestive of the mitering at the corner of a picture frame. The carpus alone has responded to this stimulus—not the distal extremity of the antibrachium. In brief this consists of a slight rearrangement of the carpal elements so that the metacarpal base of the first digit has

been shifted distad and of the fifth, both proximad and laterad, making the latter more opossable than is the pollex. The same agency that has operated to constrict the proximal part of the carpus has crowded the carpales so that these bones have become somewhat pyramidal and fit together so as to occupy the minimum of space.

In the *Zalophus* the manus externally is a rather broad and long paddle, tapering almost to a point, thicker upon the cranial or radial border and thin caudad. It is tough and elastic but the articulations of the metacarpals and phalanges are not as freely mobile as in many mammals. The palmaris longus is developed to a phenomenal degree and probably has an involuntary action in resisting an undesirable amount of extension of the manus during swimming, and by means of its insertion chiefly upon digits 1 and 5, in maintaining a slightly concave palmar surface. Extension of the pollex beyond the manual axis is largely inhibited also by all the other flexors which go to this digit and the interaction of the tendons concerned, as well as those of the remainder of the manus, is probably complicated and well developed for best efficiency. Specialization of the palmar tendons is not so strikingly marked in *Phoca*, but there is a broadening of the flexor carpi radialis to form a second deeper palmar fascia, and the middle part of the flexor digitorum communis has broadened greatly.

Such highly specialized aquatic animals as the whale and the turtle retain a short pollex, but this is not the case in the Pinnipedia. In the *Phoca* this digit is the longest and the most robust, the others being evenly and slightly subequal in sequence toward the fifth. In *Zalophus* the pollex is much the longest and much the most robust, while the fifth digit is relatively short. The flipper therefore tapers rather gradually to a point, and the entire axillary border is very thin—a condition which may be presumed of importance to the animal. The metacarpals and phalangeal bones of the Otariidae only are slightly flattened, which is a character which probably inevitably, sooner or later, follows the assumption by the manus of a paddle shape. This flattening is especially pronounced in the terminal phalanges of *Zalophus*. As mentioned elsewhere there are cartilagenous extensions of the digits in the Otariidae. The stimulus for this has evidently been at least to some degree attributable to a need for a longer manus having outstripped the lengthening ability of the phalanges The subject of the formation of these cartilages can not of course be exhausted with any such casual statement, but a number of theories which may be advanced to account for them are too speculative to merit acceptance at the present time.

There are interdigital membranes in *Phoca* while in *Zalophus* these have developed to the point where the whole manus is virtually a homogeneous paddle. This webbing need not be discussed, for it,

together with mechanisms closing the nostrils and ears, is a fundamental attribute which almost all aquatic animals develop at a relatively early stage in their aquatic evolution. The nails of the manus in *Zalophus* have deteriorated until they exist merely as horny spots within integumentary pits. As the animal has made no use of them, for scratching itself, as weapons of offense, or as tools to aid in the capture of food, they have naturally atrophied. The nails of *Phoca* are large and well formed. The external portion of the anterior limb is too short for these to be used for scratching any considerable area of the body, and even if for this use exclusively they would doubtless have become slender; and so far as is known they are of no use in the securing of food. Thus their use for scratching holes through the ice, as claimed by sealers, is the most likely theory to account for their robust development.

In the otariid the interdependence of the different parts of the posterior half of the body during terrestrial locomotion is extremely close, and in the phocid this relationship is even closer, but during the act of swimming only. It will be recalled that the hind limbs of the Otariidae are used during movement on land in a plantigrade manner by causing the axis of the sacral vertebrae to assume a vertical position, while the hind limbs are not of primary importance during natation; and that the Phocidae move upon land exactly as they would had they no limbs at all, while progression through the water is solely by means of oscillating lateral movements of the rear end. In the otariid the segments of the hind limb proximad of the heel are used upon land only as immobile supports, for they are too closely bound down to the innominates for much independent movement. Their terrestrial function therefore depends solely upon the great elasticity of the lumbar region, through the intervertebral disks. The inability of the Phocidae to use their hind limbs on land depends upon several conditions, one of which seems to be inability of the lumbar region to bend ventrad to the same degree as in the eared seals; but yet the vertebral column of the phocids is very elastic in certain directions, and *Mirounga* at least may stretch dorsad so that the backbone is bent into a veritable right angle and a rather sharp one at that. (See fig. 29.)

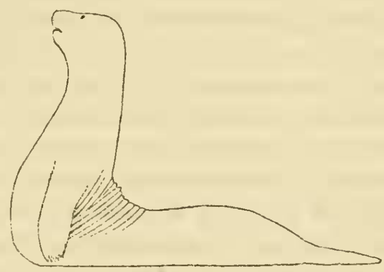

FIG. 29.—POSITION ASSUMED BY MIROUNGA ILLUSTRATING POSSIBLE DEGREE OF VERTEBRAL BENDING (AFTER A PHOTOGRAPH IN THE ILLUSTRATED LONDON NEWS OF JULY 17, 1827)

The long back muscles of *Zalophus* are essentially similar to those of a fissiped, and the hypaxial musculature is also unspecialized in

strength; but there are other muscles controlling the lumbar flexibility. These comprise chiefly the panniculus, latissimus dorsi, the posterior part of the pectoralis, rectus abdominis, and to some slight extent the other abdominal muscles. In the water, with hind quarters extended, the first three of these act as strong extensors of the humerus during propulsive action of the arm. Upon the land all of these muscles operate largely from the opposite end, assisting to the limit of their capabilities in flexing the lumbar region and making of this and the sacrum a sort of substitute femur and shank which the animal can use more expeditiously than it can the two upper segments of the limb proper. This flexure of the posterior vertebrae is used in a variety of ways besides in swimming, as in scratching, of which one can assure himself by watching the contortions of a young otariid at play.

The function of these muscles in the *Phoca* is very different. The panniculus, with fibers running rather evenly cranio-ventrad rather than converging to the axilla, is undoubtedly of assistance in the caterpillarlike mode of terrestrial progression, but it is difficult to see how the other muscles mentioned above can be of great use in such movements. In fact, an analysis of the manner in which the seal travels upon land is rather puzzling, but it is likely that the long back musculature and the psoas complex furnish most of the motive power. The rhythmic lateral movements of the hind flippers employed by these animals as the primary, and indeed sole means of propulsion in swimming have their inception in the middle thorax, as they do in the Cetacea and most fish, while the anterior thorax and the neck in large degree act as a fulcrum. The muscles of the posterior thorax and the lumbar region that are employed in these movements are primarily the enormous sacrospinal muscles, which have become massive in size but of simpler design, and accessory to these the hypaxial musculature or psoas complex. Of secondary but still of definite importance in this connection are also the latissimus dorsi and the posterior half of the pectoralis. They help to pull the posterior end of the body from side to side and operate chiefly from the deltoid crest of the humerus as a fulcrum, while the atlanto-scapularis inferior, humerotrapezius, and perhaps other muscles in conjunction, act as antagonists to prevent humeral movement. As in fish, the apaxial and hypaxial muscles of a single side act as a unit, although there is theoretically nothing to prevent them from operating with equal effectiveness in the sagittal plane as is the case in the Cetacea. The hypaxial muscles act upon the ilium and the leg, while the sacrospinalis or apaxial mass acts chiefly upon the whole pelvis, through its extensive insertion upon the "medial" face of the ilium, turned sharply lateral for just this purpose.

The pelvis of the Otariidae is somewhat weak, while that of the Phocidae is very strong and angular. For somewhat different reasons the innominate bones of these two families have become considerably differentiated in the same general direction from the normal fissiped type of pelvis, chiefly by the trailing position persistently assumed by the limbs. Most of the muscles originating from the anterior ilium are normally rotators of the femur, and as the ilium is long in fissipeds (measured from the acetabulum, 59 per cent of the innominate length in the cat) it must be important that these rotators have a long leverage. Strong rotation of the femur in pinnipeds can be of less use, however, because of the extreme shortness of this bone and the position assumed by the leg. It is true that these muscles do act as rotators of the femur in *Zalophus*, but more as abductors of the femur in *Phoca*. And in neither can the flexors of the femur nor the femoral extensors of the shank have much function as such because of the shortness of the thigh and fixed posture of the leg. All of these details conspire to obviate the need for a long ilium and the result has been an extreme shortening of this part of the innominate (32 per cent of the total length of the bone in *Zalophus* and but 16 per cent in the *Phoca*). In the fissiped the more caudal part of the innominate gives rise chiefly to muscles which extend the femur and flex the shank, and caudad of the acetabulum this portion of the pelvis is 33 per cent of the innominate length in the cat, 55 in *Zalophus*, and 74 in the *Phoca*. In the pinnipeds the whole leg is so bound down that but little extension of the femur or flexion of the shank is possible. In this order, therefore, both these groups of muscles are, by virtue of the trailing position maintained by the legs, as much if not more concerned with the actions of abduction and adduction, which is of especial use to the Phocidae. The farther the innominate extends caudad the longer will be the lever arm of these muscles and hence we find this rearward extension more pronounced in the phocids. In the otariids the pelvic muscles are used for a great variety of movements, none of which is likely of great importance to the animal, but the hind feet are flapped and rotated this way and that in their function of rudders, and the pelvic musculature is correspondingly specialized and split up into numerous divisions—the adductors to as many as six, the sartorius into two, etc. On the other hand the hind feet of *Phoca* are used for but one thing—flapping from side to side—and the musculature is correspondingly specialized, but in the direction of fusion and simplification. The gluteal mass has little to do but act upon the greater trochanter in a way to cause chiefly abduction of the femur, and the pubo-ischial muscles as adductors of the shank, but with some function of elevation and depression according as origin is from the dorsal ischium or the

pubis, and the innominate in this region has corresponding depth to allow for this. These two main movements of the leg—abduction of the thigh and adduction of the shank—are complementary in *Phoca*, for as the plantar surface of one foot is pressed against that of the other during active swimming, adduction of the right femur, for instance, assists abduction of the left shank, and the opposite.

The only other details of the innominate that merit mention consist of the dorsal spine or tuberosity of the ischium in the Phocidae extending well dorsad and developed by the narrow and somewhat tendinous origin of the superficial biceps femoris, which in the Otariidae does not arise from the innominate. Another detail is the tendency in the *Phoca* toward obliteration of the femoral process, and the development in this animal of a distinct and large process upon the ventral border of the ilium for the insertion of the psoas magnus, of such importance in its swimming.

Length of limb, comprising the sum of femur, tibia, and the distance from the tip of the second toe to the posterior border of the astragalar condyle, is without much significance in the Pinnipedia because so much of the limb is within the body. However, as compared to body length this item is 104 per cent in the cat, 62 in *Zalophus*, and 74 in *Phoca*.

The femur in this order has become very short indeed. Whereas this bone in the cat is 35 per cent of the body length, in the *Zalophus* it is but 22 and the *Phoca* 29 per cent. In function it plays a very minor part as a segment of the limb and I regard its diminution in size as intimately correlated with the shortening of the ilium and consequent reduction in the length of the muscles between these two points as well as by the great reduction in femoral mobility. I am not prepared to say that the position of the femur is uniform in the Otariidae, but at least in the *Zalopus* dissected the static position of this bone was apparently at a cranio-lateral inclination forming an angle with the body axis of about 45°, but markedly rotated. In other words, the femur is normally carried very strongly flexed and rotated cranio-mediad. (See fig. 30.) In contrast to this the femur of the *Phoca* was directed a trifle caudad of laterad to the body axis and there was no marked rotation. As a result of these postures the muscles that pull cranio-mediad (the gluteal complex) upon the greater trochanter of the otariid chiefly rotate the femur, with the final result on land of turning the toes outward. This same action in the *Phoca* results in the abduction and extension of the femur. Another result of these femoral positions is that in reality the effective length of the otariid leg is less than the sum of the tibia and pes, while in the phocid it is greater. The arc of effective flexion and extension of the femur seems to be only about 25° in *Zalophus* and 30° in *Phoca*, with the amount of flexion in the former slightly greater

than extension. Abduction and adduction is greater—possibly through as much as 40°.

The flatness of the pinniped femur is probably attributable to a variety of stimuli—the lack of need for antero-posterior thickness, the need for a greater trochanter extending well laterad of the

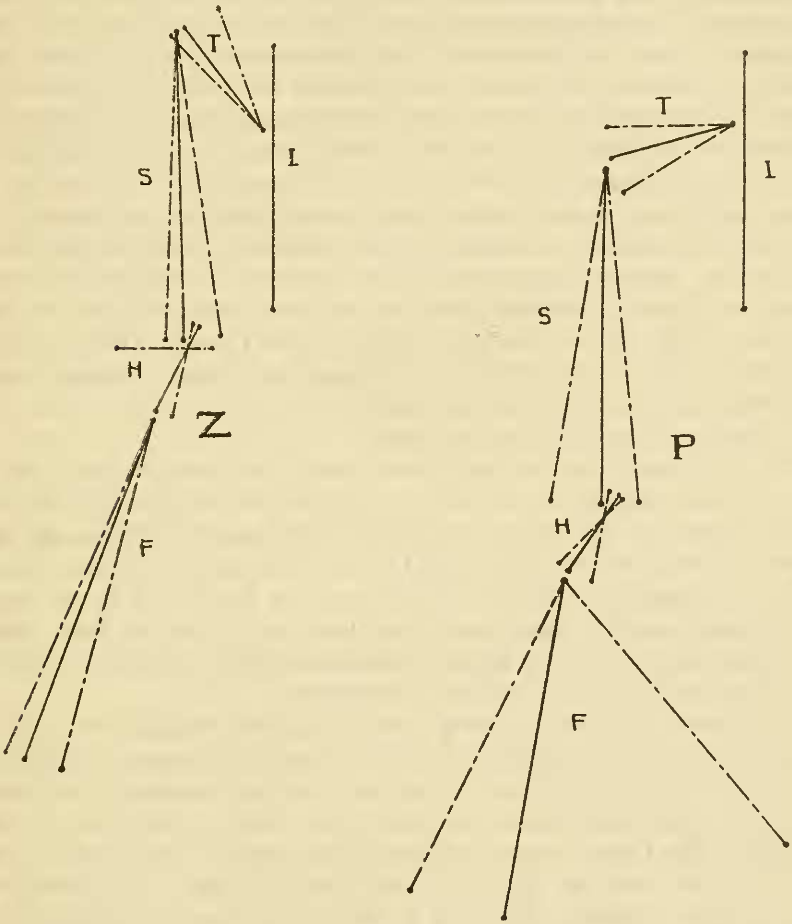

FIG. 30.—DIAGRAM ILLUSTRATING APPROXIMATE STATIC POSTURE (SOLID LINES) AND DEGREE OF POSSIBLE MOVEMENT (BROKEN LINES) IN LIFE OF EACH JOINTED SEGMENT OF THE POSTERIOR LIMBS OF ZALOLPHUS (*Z*) AND PHOCA HISPIDA (*P*). *I*, INNOMINATE; *T*, THIGH; *S*, SHANK; *H*, HEEL (ASTRAGALUS AND CALCANEUM); AND *F*, REMAINDER OF FOOT

acetabulum and for a broad distal extremity. The greater trochanter of both animals is very similar. In the *Zalophus* the trochanteric fossa is a slight concavity while in *Phoca* it is a very deep pit because in this animal the muscles inserting in its vicinity are more specialized in order that all may perform practically the same act and their insertions are more circumscribed and more strictly

tendinous. The lesser trochanter, occurring in the Otariidae only, is rather small and supports narrow insertions of the sixth adductor, pectineus, and psoas magnus and iliacus element. In *Phoca* the only one of these muscles which insert in this vicinity is the pectineus, and this more broadly. The more decided and sharp epicondylar ridges of *Phoca* are doubtless attributable to the stronger action of the muscles originating therefrom. In the skeletons at hand the patellar " fossa " of the otariid is undifferentiated and this part of the femur is convex. In the sea lion dissected the patella also rested at the junction of the thigh with the shank rather than upon the femur, because of the flexed position of the latter bone. In some other members of the Otariidae, however, there is considerable variation in this detail, and I shall not attempt to account for this condition. In the *Phoca* there is a deep, concave patellar fossa in the usual situation. As previously noted, a line passing through the center of the two femoral condyles describes an angle with the axis of the shaft of about 79° in *Zalophus* and 63° in the *Phoca*. This is attributable to the lateral condyle being somewhat more proximad than the medial in the otariid, and much more so in the phocid. This will be discussed in relation to the shank.

The pinniped tibia has experienced some shortening but not nearly to the same degree as the femur. In the cat this bone is 36 per cent of the body length, in the *Zalophus* 22 and in the *Phoca* 29 per cent. From another angle, the femur of the cat is 97 per cent of the tibia length, in the *Zalophus* 50 and in the *Phoca* 40 per cent. The shank is of the usual carnivore type, that of the sea lion rather straight except that the fibula is slightly rotated, and of the phocid more curved, but with the fibula nonrotated.

The head of the tibia differs from that of the ordinary fissiped in having the anterior edge quite sharply angular instead of sloping, which is undoubtedly due to the fact that in pinnipeds the shank is never really extended in respect to the thigh. The head of the fibula in the *Phoca* is even and continuous with the tibial head, but in *Zalophus* it slopes directly distad from the latter and is continuous in this direction with the shaft. This is a provision in the otariid for excessive flexion of the shank in respect to the thigh, the femur fitting down over the sloping head of the fibula in a sharper angle than is mechanically possible in the phocid. As mentioned, the lateral femoral condyle of *Zalophus* is situated a bit more proximad than the medial, but in the markedly flexed static position of the shank the only effect which this condylar position has is to place the shank in a more pronated posture. The lateral tuberosity of the shank in this animal, however, is placed more distad than the medial, and this has the effect, in the position assumed by the limb segments, of elevating the shank and ankle toward the dorsum. The

disparity between the positions of the femoral condyles of *Phoca* is considerably more marked, but in the somewhat more extended position in which the femur of this animal rests this has the same effect of elevating the ankle but to a more marked degree, caused by the more sloping articular head of the shank. This marked elevation of the phocid pes is very characteristic, and I have seen an animal sleeping for an hour or more with the hind feet elevated in a position which to any other mammal would surely be the height of discomfort.

A pinniped peculiarity, or at least one that is not shared by the majority of fissipeds, is found in the knee joint. The medial or tibial collateral ligament is not attached at a point about one-tenth the distance from the knee to the ankle, as in the cat, but at a point in *Zalophus* about two-fifths, and in the *Phoca* about one-quarter, this distance. In connection with a loose capsule of the joint the result is that in the Pinnipedia there is permitted at least 40° of rotation of the shank with respect to the femur (in the partially dissected specimens), the fibular collateral ligament being the pivotal center. This I believe to have been brought about chiefly by the fact that during most of the time the hind feet of both the otariids and phocids are maintained with their axes practically continuous with those of the shanks, and in this position rotational movements of the feet would be transmitted to a considerable extent directly to the knees. In the *Zalophus* only, such rotation of the shank, in the direction of supination, has the effect of adducting the ankle. Flexion and extension of the pinniped shank is largely inhibited, especially in the otariid, by the muscles which bind it down so closely and by the limits of elasticity of the integument in which it is inclosed. These movements are possible through an arc apparently of only about 15° in the *Phoca* and even less in *Zalophus*.

The fibular head of the *Zalophus* is placed more caudad of the shank in respect to the direction of the femoral articulation than is the case with Phoca—almost directly caudad of the lateral tuberosity in the former, and caudo-laterad, at an angle of 45° in the latter. In the phocid the tibia is straight, so that the ankle joint "toes out" to an angle of about 45° to the transverse axis of the proximal articular surface of the shank. In the otariid, however, there is rotation of the fibula so that considered in the same light, the transverse axis of the ankle joint is parallel to that of the knee. This means that were these plantigrade fissipeds, the foot of the *Phoca* would at rest point straight laterad and of the *Zalophus* latero-craniad at about 45°, which in fact it very nearly does. In the *Zalophus* the fibula ends somewhat proximad of the tibia, and the articular surface of the latter is several times the larger. In *Phoca*

these bones end even and the articular surface of the fibula is almost as extensive as of the tibia. *Zalophus* has few malleolar grooves which are broad and shallow, but in *Phoca* these are exceedingly deep, narrow, and pulley-like, which form has undoubtedly been developed by the constant see-saw movements of the tendons performing precisely repeated motions during swimming.

The shank bones, especially the fibula, of *Phoca* are more ridged and show more indications of every kind of strength of muscle. Perhaps the most remarkable muscular modification of this region is without osteological indications, however, and includes the hamstring muscles—biceps femoris, gracilis, semimembranosus, and semitendinosus. In the *Zalophus* the biceps is of a very remarkable rhomboid shape. Insertion of the superficial sheet is fascial over the proximal four-fifths of the shank, and origin is practically as extensive over the anterior caudal spines. The result is that the shank is bound down nearly in contact with the innominate and its mobility is almost inhibited. Equally effective in this function but less strikingly modified are the gracilis, semimembranosus and semitendinosus whose insertions are distributed over the distal two-thirds of the shank, and with origins confined to the posterior part of the innominate. In *Phoca*, whose hind limb is apparently useless for all purposes save lateral oscillations, one would expect the biceps to be even more modified for binding down the shank, but such is not the case. The muscle is of prime importance in adduction of the shank, so although insertion is extensive over the shank (the proximal seven-eighths) for long leverage, the muscle is robust and tapers to a tendinous origin from the superior spine of the ischium, where it can act to good advantage as an adductor, as well as an elevator to some extent. The other hamstring muscles are also strong, and disposed in insertion much as in *Zalophus;* but origin, especially of the anterior semitendinous, is not so entirely confined to the posterior border of the innominate, thus giving a slightly greater length to these muscles. The hamstring group are the only muscles which can adduct the shank with any real power, and hence, are of fundamental importance to the swimming of *Phoca*. They act in the most intimate cooperation with the muscles of the lower back in performing the lateral oscillations of the posterior end, and it must not be forgotten that because of the adpressed palmer position of the feet, adduction of the ankle and foot of one side may furnish much of the impulse to abduct those of the opposite side.

As mentioned elsewhere, there has been a slight movement proximad of the origins of the flexor digitorum longus, and peronei longus and brevis of these pinnipeds, and a movement distad of the origins of the flexor hallucis longus and extensor digitorum longus. The stimuli for these changes are obscure, however. Because the muscles of the

Zalophus were emaciated and those of the *Phoca* very full, little comparison of the strength of the shank muscles could be made. Details of note, however, were the presence in *Phoca* only of a gastrocnemius lateralis and absence of the soleus, and strength of the gastrocnemius medialis and flexor hallucis longus. These differences are, of course, related to variations in foot action, but most of them in an obscure manner.

The effective length of the bony part of the foot, measured from the posterior margin of the astragalar condyle for a cat, is 34, the *Zalophus* 28, and *Phoca* 34 per cent of the body length. Thus the osseous foot of the last has not shrunken in relation to the trunk length as has the rest of the limb, and that of the otariid has done so but slightly. Or from a more likely aspect, the foot of both animals has experienced a secondary increase in size following a very marked, primary decrease in the length of the rest of the limb, especially the femur. This increase of foot length, however, has not been sufficiently rapid in the Otariidae to keep pace with the needs of the animal, and there has been an extension of the digits by means of cartilagenous rods and slightly more circumscribed interdigital membranes. The part of the pes distad of the bones is very flexible and the cartilages are prolonged distad of the interdigital membranes to a degree that seems entirely useless, and one which at present seems very inefficient.

The measurement from the tip of the longest otariid toe (externally) to the border of the astragalar condyle is 36 per cent of the body length, which is the same as in the phocid. In the latter, however, the interdigital membrane extends between the toes in a much more effective manner, and there is no flexibility distad, for there are no cartilagenous extensions of the digits. But the foot is relatively larger than in the otariid, and the measurement from the external toe tip, as above, constitutes the same proportion of the trunk length as in the eared seal. Either the increase in foot size has kept pace with the needs of the animal, or, as seems by no means unlikely, the Phocidae lack the ability so readily to develop digital cartilages.

As with the manus the plantar surface of the otariid is bare and wrinkled, and of the phocids, as well haired as the remainder of the foot. The first and fifth toes of the former animal have minute nails, sunk in pits of the integument, but the nails of the other three digits are long, nearly straight, and very slender, as are those of all five digits of the phocid. The otariid frequently folds back the part of the pes distad of the bones, leaving the three long nails projecting, and with these vigorously scratches all parts of the body. I see no other way in which they could be utilized and agree with F. Wood Jones (1925) that the retention of real nails upon the three

middle digits of the pes in the Otariidae is solely because of this fuction of scratching and combing the hair. I am, however, at somewhat of a loss to explain the retention upon all the digits of the pes in *Phoca* of such long nails. Jones believes that the position of the pes of this animal inhibits any appreciable scratching by the nails, to which I subscribe, and that the limited toilet is then performed by the claws of the manus, in which I do not agree, for any such action by the manus is well nigh as limited as by the pes. And yet it seems that the claws must be of some definite use, for the Phocidae are certainly sufficiently ancient for their claws to have disappeared entirely were they not of practical value to the animal in some respects.

The details of pedal movement are not easily followed either in the reconstructed foot, or from the embalmed specimen after most of the tissue and many of the muscles have been cut away. The ankle joint of *Zalophus* is such that the tibial facet of the astragalus dips but slightly medioventrad from the horizontal, while in *Phoca* it and the fibular facet are both at 45°. The result is that if one hold the shank vertical and bend the foot, the transverse plane of the phocid foot is at practically 90° to the shank, while in the otariid it is nearer 45°. In other words, in such a free limb, disarticulated from the body, the tendency is for merely the lateral border of the foot to rest upon the ground—not the entire sole. The full plantigrade position may be assumed, however, either by forced pronation through the ankle joint and the tarsal articulations, or more likely by the slight adduction of the proximal shank toward a knock-kneed position, the rotation of the shank at the knee joint in a direction toward pronation, and of the femur in a direction toward supination. This is less complicated than it sounds; but the strange part is that could *Phoca* place the sole flat upon the ground in the same fashion as can *Zalophus*, none of this rotation or adduction of the shank and femur would be needed. In the otariid the crotch, or angle between the hind limb and the tail, was at the calcaneal tip, while in the phocid this point was situated some 20 mm. farther distad; so the difference in this respect is not by any means so great as alone to prevent the phocid foot from assuming a plantigrade posture did other anatomical details allow it to do so. Murie (1874) considered that the phocid's " incapacity to use its hind foot on land depends more on the different proportion of femur to leg bones and lowered attachment of integumentary caudal expansion than to absolute difference in the construction of the bones forming the ankle joint"; but none of the three points mentioned are of primary importance in inhibiting such an act.

As already mentioned, the static position of the trailing feet when submerged seems to be with the palms steeply V-shaped in *Zalophus*,

and the opposite in *Phoca;* but adpression of the palms is assumed with ease in both animals, and much pronation and supination is possible from this position. There is but slight pronation or supination through the actual ankle joint of either animal, but the articulations distad are loose and movement much facilitated, especially in the phocid.

In the *Zalophus* the flexion-extension action of the ankle proper is through an arc of about 75° and of the tarsus through 10° or 15°, allowing the foot to assume a plantigrade position or to trail in the same plane with the axis of the shank. In *Phoca*, however, conditions are very different. Movement at the ankle joint is from the extreme trailing position through an arc of only 30° toward plantigradism, the inhibitional factor being the tendon of the flexor hallucis longus, as discussed later. In the oscillating swimming movements of the feet of this animal it is requisite, however, that there be more play and flexibility than such an ankle joint will allow, and this is attained through the articulation between the astragalus-calcaneum and centrale-cuboid. And this joint, called the tarsal joint, is actually more flexible than that of the true ankle, this being through an arc of 65° or more. The result is that the mechanism of the phocid pes is very handlike, and the tarsus may be flexed at a right angle to the axis of the heel, thus assisting by a follow-through movement the adductor motion of the distal leg in swimming. In the otariid the tibial facet of the astragalus is prolonged onto the neck but stops short of the junction with the heel. In the phocid this condition is just reversed, showing that the joint is considerably better fitted for maintaining the foot perpetually in a trailing posture. In the entire specimens, however, there is no appreciable difference in this respect, which is a further instance of the fact that from observation one can not always tell what a structure is best fitted to do.

Comparative osteology is not yet at the point where the significance of slight changes in the interrelationship of the tarsal bones are perfectly understood, and not a great deal can be said with confidence regarding the structure of the otariid tarsus. That of *Phoca*, however, is somewhat more illuminating. The calcaneum, is rather weak but is deeply grooved for the passage of the peroneal tendons. Partly accountable for the lack of strength in the posterior process of this bone is the fact that the phocid has no soleus and that in this animal as well as the *Zalophus* the plantaris is entirely distinct from the "tendo calcaneus" and passes mediad to it. In fact, in view of the permanently extended position of the foot, together with the development of the flexor hallucis longus, one would rather expect to find that this process was still more reduced in the earless seal.

It is, however, in the phocid astragalus that interest chiefly centers. Its articular facets differ from those of *Zalophus* as already discussed, but in addition there extends caudad a large, long process—an accessory heel, as long and almost as deep as that of the calcaneum. It is broadly grooved caudo-ventrad for the passage of the stout tendon of the flexor hallucis longus, and it is the strong tension of this muscle that primarily, if not solely, inhibits the assumption of a plantigrade posture by the foot in this animal. This is, perhaps, the most significant single detail of the specialization of the Phocidae. Why is it that the hallucis longus was so highly and peculiarly developed to flex the foot with a considerable leverage to a somewhat excessive degree rather than the muscles going to the calcaneum, with equal leverage ready to hand is a puzzling circumstance. It is likely, however, that one important factor was that the hallucis, as it occurs in this animal, is also well fitted for facile flexion of the digits. In its distal portion also the astragalus differs much from the condition in *Zalophus*. Whereas in the latter the facet for articulation with the centrale is prominent and highly convex, and with a protuberant process mediad, in the *Phoca* this facet—very much smaller—is flattish and somewhat irregular. In addition, the distal part of the bone is rendered much more narrow by the absence of the medial process, probably caused partly by the more dorsal position in this animal of the tendons of the extensor hallucis and tibialis anticus, and partly by the reduction in width of this part of the tarsus. By the shape of this facet and its relation in regard to the cuboid the excessive amount of movement of which this tarsal joint is found to be capable is evidently facilitated, and the narrowness of the tarsus at this point permits a certain amount of motion in the transverse plane. Another point worth mention is that as the calcaneum and astragalus are of the same length, they can be, and are, closely bound together by ligaments and therefore together constitute an unusually solid base for the remainder of the pes.

The lateral side of the cuboid has a groove for the passage of the peroneus longus tendon that is completely roofed over by a process of the bone in contact with metatarsus 5. These tarsal grooves, absent as such in *Zalophus* and formed exclusively by the peroneal muscles in *Phoca*, are an indication of unusual and persistently recurring contraction of these muscles. In the trailing position in which the feet of this animal are always carried, action of the peroneal group results exclusively, if we except the usual binding action upon the tarsal bones of the peroneus longus, in elevation of the feet, and therefore to some slight degree as an aid to the spreading of the digits. These facts suggest that there is somewhat more of a twisting, sculling movement of the rear flippers in swimming than one is able to distinguish during observation of a live individual.

The proximal ends of the metatarsal bones in both animals seem to have been subjected to transverse pressure, indicating that this part of the foot may be narrower than in the ancestral forms. In *Zalophus* this has resulted in making the metatarsal bases narrower and deeper, but in *Phoca* merely in excessive crowding, with numerous short processes filling all available spaces. A stimulus for this sort of interlocking tarso-metatarsal articulations has probably also been furnished by the fact that the feet of this animal are useless upon land. After removal of the integument it is found that the otariid metatarsus 1 and 2 are bound closely together, while there is a slight amount of transverse play between the others; in the phocid, 1 with 2 and 4 with 5 are so bound, and these, as two units, may be slightly moved transversely from 3. As in the usual land mammal, however, transverse movement of the metatarsals during the spreading of the digits is found to be really very slight.

In both pinnipeds there has been a strengthening and lengthening of the first and fifth digits and their metatarsals which is of decided use in stiffening both borders of the pes while it is expanded and being forced against the water, but this seems to have been carried to a greater extreme in *Zalophus* than can now be of real use. There is a suggestion of flattening of the phalanges, especially upon the plantar aspect in *Zalophus*, and to some extent in all its digits and metatarsals. This is specialization in the expected direction for an aquatic mammal.

There is no especial provision, in the way of arrangement of pedal tendons, for the spreading of the otariid foot and the muscles of the foot proper appear to be quite weak. This is not surprising, but one is mildly astonished to be unable to distinguish any special provision in the phocid either, although the plantar muscles are rather strong. From manipulating the pes, however, it seems that spreading the digits does not in this animal consist of purely transverse impulses, but that this action is slightly oblique and consists very largely of extending the first digit and moderately flexing the fifth at the metatarsal-phalangeal joint only. Thus interrelated action between certain of the flexor and extensor tendons of the digits would supply the activating power for spreading the toes, but the conformation of these tendons does not disclose their identity.

CONCLUSIONS

A discussion of pinniped relationship is of decided secondary importance in the present paper, but it is felt that it is desirable to offer some consideration of this question, as well as some weighing from a phylogenetic viewpoint of the anatomical evidence encountered. The order may be characterized as follows:

PINNIPEDIA

Amphibious mammals of fusiform shape and with short tails. The elbow and knee always well within the body contour and with the feet webbed and paddle-shaped. The digits are always five and the fifth toe of the pes is approxmiately equal to the first, both being greater than the three middle toes. The mammae number either two or four. The incisors in living forms are always fewer than 3/3 and the cheek teeth, variable in number, generally consist of four premolars and one molar, but occasionally there are two or three molars (*Callotaria*). The molariform teeth never have more than two roots and there is no differentiated carnassial tooth, all these teeth being uniform in character. The milk teeth are small and simple and are shed at an early age. The lachrymal bone is almost always absent; when present it is small and within the orbit. The auditał bulla is composite. There is no clavicle. The pre-acetabular length of the innominate is apparently always much less than the postacetabular, at least in living forms. The humerus is massive and the bones of the forearm very broad. The femur is much reduced in length and is flattened. There is an os penis. The brain is large and its convolutions complex. The kidneys are lobulated and in adults there are large hepatic sinuses of the vena cava.[6] There are no Cowper's glands.

OTARIIDAE

External ear small. Both fore and hind feet used extensively during terrestrial locomotion. Area of forefeet great, this extremity being plainly indicated as the more definitely developed for aquatic propulsion, and the axilla is situated at mid forearm. The hind feet assume a plantigrade posture during terrestrial locomotion and the astragalus is without a conspicuous posterior extension. A cartilaginous extension to each digit occurs and the palms and soles are naked. The nails of the forefeet and those of the first and fifth digits of the hind feet are vestigeal. The testes are scrotal in the adult male. The tooth formula is:

$$i. \frac{3}{2}, c. \frac{1}{1}, pm. \frac{4}{4}, m. \frac{1 \text{ or } 2}{1, 2, \text{ or } 3};$$

total 34 to 38. The canines are but moderately developed. The molariform teeth have a single main cusp and at times a cingulum, with occasionally slightly developed anterior and posterior accessory cusps. The skull has a well-developed postorbital process, normally an alisphenoid canal, a mastoid that is usually noninflated, and a mastoid process that is conspicuous and continuous with the paroccipital

[6] The presence of these sinuses is merely presumed to be uniform within this order.

process. The ossification of the border of the auditory meatus is regular and uninterrupted in fetuses[7] and the occipital condyles are usually narrow. The vertebral spines of the anterior thorax are well developed. The scapula is subtriangular (never falciform) and with a distinct acromial process. The greater tuberosity of the humerus is higher than the lesser and there is no entepicondylar foramen. The ilium is but slightly curved—not markedly and abruptly bent laterad. The femur has a lesser trochanter.

PHOCIDAE

There is no external ear. Neither fore nor hind feet are used as primary aids in terrestrial locomotion. The area of the forefeet is reduced and the axilla falls opposite the wrist. The external surface of the hind feet is increased, relative to the length of the leg, these being plainly indicated as the chief means of aquatic propulsion rather than the forefeet. The astragalus has a posterior extension as long as that of the calcaneum, and the foot is prevented from assuming a plantigrade posture by the unusual tension of the flexor hallucis longus muscle. There are no cartilaginous prolongations of the digits, and the palms and soles are usually well haired. The nails are well formed and never vestigeal. The testes are abdominal in the adult male. The tooth formula is:

$$i.\ \frac{2 \text{ or } 3}{1 \text{ or } 2},\ c.\ \frac{1}{1},\ pm.\ \frac{4}{4},\ m.\ \frac{0,\ 1 \text{ or } 2}{0,\ 1 \text{ or } 2};$$

total 26 to 38. The canines are rather poorly to moderately developed. The skull has no postorbital process, and there is no alisphenoid canal. The mastoid is relatively inflated and the mastoid process either poorly defined or else not continuous with the paroccipital process. The ossification of the border of the auditory meatus is irregular and interrupted in the fetal state[8] and the occipital condyles are usually broad. The vertebral spines of the anterior thorax are very poorly developed. The scapula is often somewhat falciform and the acromial process is not well marked. The lesser tuberosity of the humerus is usually higher than the greater, and there is often present an entepicondylar foramen. The ilium is markedly and abruptly bent laterad. There is no femoral lesser trochanter.

Many other characters of differentiation exist, but for the most part these are slight and not so well suited for purposes of diagnosis. In addition, a few of the above characters need verification

[7] In the Otariidae this was determined for *Callorhinus* only, but it is probably a uniform character.

[8] Determined in the case of *Phoca vitulina* only.

regarding their invariable presence in or absence from the two groups before they can be accepted without reservation.

Little account has been taken of the Odobenidae or walruses in the present paper, but it may be mentioned that morphologically they appear to be little more than specialized otariids, distinguishable chiefly by the enormous development of the upper canines (which has been followed by necessary adjustments in the bones of the skull) and compensating reduction in number of the remainder of the teeth, as well as a change in their pattern to conform to special food; disappearance of the external ear, and a change in the limbs, making these in some respects intermediate between those of the Otariidae and Phocidae. There is no doubt whatever that the relationship of the walruses is much nearer to the eared than to the earless seal stem.

Wortman (1894) believed that the Pinnipedia are derived from the Oxyaenidae, a phylum of inadaptive creodonts. Matthew (1909) has argued convincingly against this thesis, and ascribes ancestry to the arctoid fissipeds, but Kellogg (1922) presents evidence which apparently renders the latter as well as the former theory unlikely.

Remains of unquestionable Pinnipedia of both otariid and phocid affinities have been found from the Miocene, but from no deposits of older age, and these remains are of pinnipeds which had already reached a high degree of aquatic specialization. Hence it is certain that this order diverged from terrestrial fissipeds at a very early time. But until far more and considerably older remains of this order than are now available are at hand, any attempt to allocate the pinniped relationship and ancestry is too speculative for acceptance. All that seems certain is that the pinniped precursor was of carnivore stock, with probably some affinities with that large aggregation of diverse predators known as the adaptive creodonts. In view of the profound changes which had already taken place in pinnipeds of the Miocene, the origin of this stock was "probably not later than the Eocene" (Kellogg, 1922) and possibly earlier.

There has been much conjecture regarding the derivation of the pinniped families. Many investigators have considered that the order is diphyletic or biserial, and some (as Mivart, 1885) have favored the theory that the Otariidae are descended from an ursine, and the Phocidae from a lutrine, ancestor, and have presented anatomical data in support of such reasoning; but this is not convincing and evidence of much weight may be marshaled against it. It is hardly necessary to review this question in detail in the present connection, but it has seemed to me rather unprofitable to consider seriously the probable relationship of any family of pinnipeds with any of existing fissipeds. Furthermore, the otariid stock is considered

to be older than the ursine, as mentioned by Kellogg (1922), and the phocid line may well prove to antedate the lutrine.

At any rate the typical otariid is now very different from the typical phocid of the present day. Comparative anatomy should contribute much evidence informative of the degree of phyletic divergence that they have experienced, and it is found to do so, but the evidence is often of so contradictory a character that it is far less satisfactory than had been hoped. The significance of some of the more important of the differences as they exist, however, may be discussed.

The methods of swimming now employed by the otariids and phocids are fundamentally different. These differences may date from the time when the first ancestors of the two families managed to swim across a river, or it is very possible that the ancestral otariid and ancestral phocid followed the same method of swimming until they were as well fitted for aquatic life as, say, the otter (*Lutra*), or conceivably more so. The two stocks then acquired steadily increasing adaptations, but of diverging sorts, throughout the ages, or else one or the other of them experienced retrogressive changes of indeterminate duration. In other words, it is not impossible that there was a considerable stretch of time when the otariid employed also the hind feet and the phocid also the forefeet primarily as accessory propulsive organs, and that this time lasted sufficiently long for strong anatomical evidence of the fact to remain at the present day. And indications, as enumerated shortly, are not lacking that retrogressive changes of this sort may actually have been experienced by both families. Furthermore, it is extremely probable that all parts of the body which show aquatic modifications have not evolved at the same rate or velocity. Thus, the fact that the external ear of the phocid has disappeared while that of the otariid has not may merely indicate that slight differences in habits have operated to retain the external ear in the latter.

As evidence for or against close relationship of the two pinniped stocks such matters as general body form, external details of the eyes, nose, and ears migration distad of the external axilla and of the crotch of the posterior limb and craniad of the anterior border of the pectoralis origin, form of the innominate, and shortening of certain segments of the limb, are not particularly illuminating, for these are items which conform to usual or eventual requirements of aquatic adaptation and they might be due largely to convergence. On the whole, however, *Phoca* exhibits in these respects a somewhat greater divergence from fissiped conditions than does *Zalophus*.

The following differences may be considered as attributable chiefly to the dissimilarity in the modes of progression characteristic of the two families: differences in the form of the neck; in the length

and general form of the manus; in hypaxial and sacrospinal musculature, the latter being largely instrumental in causing differences in the processes of the vertebrae and in the conformation of the ilium; in the diversification of the hip muscles of *Zalophus* and their tendency toward fusion in *Phoca*; the astragalar extension in *Phoca* and peculiarity of the flexor hallucis longus muscle; and of the flexibility of the tarsal joint in *Phoca*.

Differences which I consider might be attributed either to aquatic adaptation of the two sorts shown, or to phylogenetic influences, consist of the dissimilarities exhibited in the occipital musculature, sternomastoid, cephalohumeral, humerotrapezius, rectus abdominis, deltoid, the origin of the triceps longus and of adjoining muscles, the presence of an episubcapularis in *Zalophus* only and of an abductor digiti quinti longus in the *Phoca* only, the differences shown by the humeral tuberosities, the palmaris longus, and the iliacus.

Differences which may be laid chiefly to phylogenetic influences rather than to aquatic adaptation consist of many of the details of the skull, the presence of the complex division of the longus colli in *Zalophus* only, and likely the absence in this genus of the quadratus femoris, and of the presence in *Zalophus* only of the soleus.

Resemblances of a quality which one might reasonably consider to constitute evidence of close relationship comprise some features of the triceps complex, similarity in the migration of attachments of the brachial muscles, broadening of the antibrachial bones, resemblance shown by the deeper division of the biceps femoris, the occurrence of a hepatic venous sinus, and possibly of the details of the tibial collateral ligament and plantaris tendon, and of the presence of a superior division of the atlantoscapularis, although the latter may likely be of little import.

It has been mentioned that dissimilarities in the external ear, mode of swimming, and of terrestrial locomotion may be interpreted as evidence that *Phoca* is the more highly adapted to aquatic life and hence has diverged more from the fissiped type. In contrast to this, the thesis that *Zalophus* is the one that has traveled farther from the typical terrestrial carnivore is supported by the greater tendency toward "telescoping" of its skull, cartilagenous extensions of the digits, the greater tendency toward flattening exhibited by the pedal phalanges of this pinniped, and possibly by the development of the nails.

In scrutinizing the anatomical details encountered there occur a number of questions which are not readily answered, as enumerated below. To these the reader, if he be so minded, may add the query as to why such arm muscles as the triceps and deltoid are so specialized or well developed in *Phoca*. This I am not including for the reason that I am inclined to ascribe this condition to possible

antagonistic work which the brachial muscles of this animal must needs perform during swimming movements by the hinder portion of the body. These questions, then, may be propounded as follows. Given the habits and form of the two animals dissected, then:

1. Why should the crotch of the posterior limb be located practically as far distad in *Zalophus* as in *Phoca?*

2. Why should the superficial division of the biceps femoris be developed in *Zalophus* to bind down the shank more firmly than it does in *Phoca?*

3. Why should the excessively shortened femur be relatively of the same length in both?

4. Why should the pes of *Zalophus* be in most respects more specialized than is *Phoca?*

5. Why should there be such large cartilagenous extensions of the pedal digits in *Zalophus* but none in *Phoca*, which apparently would have more use for them.

If one accept the thesis of a certain amount of retrogressive evolution having taken place then these five points are easily explainable. For the sake of argument then, let us presume that at one time before the Phocidae used the posterior limbs so exclusively for aquatic locomotion they made great use of the forefeet also. The adjoining muscles would then become highly specialized, a condition which might survive as a relic after disuse had caused great reduction in the size of the forelimb. Similarly, then, it may also be argued that the hind limb of *Zalophus* may conceivably have been a primary means of aquatic progression in the very distant past, and it then might readily have acquired the puzzling details listed above, which subsequent relative disuse has failed to obliterate. In support of such argument is the seeming fact that the terminal digital cartilages of the pes of a juvenile *Zalophus* appear to be relatively better developed than in an adult.

This hypothesis of retrogressive evolution has been presented merely because it largely explains matters, and it is the only one which appears to do so. I may eventually come to accept it but at the present time I am, nevertheless, far from convinced that this is the proper explanation.

It is seen that the present contribution sheds little or no light upon the question of whether the Otariidae or the Phocidae is the "older" family. The evidence is conflicting and the proper weight to accord details of variation is, and probably always will be, a moot question. It is felt, however, that this evidence points to the probability that the Otariidae, although not necessarily the better (or as well) equipped for an aquatic existence, have perhaps departed widely from a typical terrestrial condition in more numerous and profound respects than have the Phocidae.

BIBLIOGRAPHY

ALLEN, HARRISON.

1888. Materials for a memoir on animal locomotion. Extracted from report on Muybridge work at Univ. of Pa., pp. 35–104.

ALLEN, J. A.

1870–71. The eared seals. Bull. Mus. Comp. Zoöl., vol. 2, pp. 69–73.

1880. History of North American pinnipeds. Misc. Publ. 12, Dept. of Interior, Washington, pp. 1–785.

1902. The hair seals (family Phocidae) of the North Pacific Ocean and Bering Sea. Bull. Amer. Mus. Nat. Hist., vol. 16, art. 34, pp. 459–499.

BEDDARD, F. E.

1890. On the structure of Hooker's sea lion. Trans. Zool. Soc. London, vol. 12, pp. 369–380.

CUNNINGHAM, D. J.

1923. Textbook of anatomy. Ed. 5, Wood and Co., New York, pp. 1–1577.

DUVERNOY, G. L.

1822. Recherches anatomique sur les organes du movement du phoque commun, Phoca vitulina, L. Mem. Mus. Hist. Nat. Paris, vol. 9, pp. 49–70, 165–189.

FLOWER, W. H.

1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. Proc. Zool. Soc. London, pp. 4–37.

1876. An introduction to the osteology of the mammalia. Macmillan and Co., London, pp. 1–344.

FLOWER, W. H. and R. LYDEKKER.

1891. An introduction to the study of mammals living and extinct. London, pp. 1–763.

GRAY, HENRY.

1903. Gray's anatomy, descriptive and surgical, Ed. 13, pp. 1–1249.

GREGORY, W. K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1–524.

HEPBURN, D.

1909. Observations on the anatomy of the Weddell seal (Leptonychotes weddelli). Scottish Nat. Antarc. Exped., 8, Trans. Royal Soc. Edinb., vol. 47, pp. 57–63.

HOWELL, A. BRAZIER.

1926. Anatomy of the wood rat. Monog. 1, Amer. Soc. Mamm., pp. 1–225.

JAYNE, H.

1898. Mammalian anatomy, a preparation for human and comparative anatomy. Part 1. The skeleton of the cat. J. B. Lippincott & Co., Phila., pp. 1–816.

JONES, F. WOOD.

1925. The mammalian toilet and some considerations arising from it. Royal Soc. Tasmania, Papers & Proc., pp. 14–62.

KAMPEN, P. N. VAN

1905. Die Tympanalgegend des Saugethierschadels. Morph. Jahrb., vol. 34, pp. 321–722.

KELLOGG, REMINGTON
1922. Pinnipeds from Miocene and Pleistocene deposits of California. A description of a new genus and species of sea lion from the Temblor, together with seal remains from the Santa Margarita and San Pedro formations and a résumé of current theories regarding origin of the Pinnipedia. Univ. Calif. Publ. Geol. Sci., vol. 13, No. 4, pp. 23–132.
1925. Structure of the flipper of a Pliocene pinniped from San Diego County, California. No. 5. Additions to the Tertiary history of the pelagic mammals of the Pacific Coast of North America. Contributions to Paleontology, Carnegie Inst. Wash., Publ. 348, pp. 97–116.

LEBOUCQ, H.
1889. Recherches sur la morphologie de la main chez les mammiferes marins. Archiv. de Biol., vol. 9, pp. 571–648.

LUCAE, J. C. G.
1872. Die Robbe und die Otter in ihrem Knocken und Muskelskelet. Abhandl. Senchenberg. Naturf. Geselsch., vol. 8, pp. 277–378.

MATTHEW, W. D.
1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pp. 413–417.

MILLER, W. C. S.
1887. The myology of the Pinnipedia. Appendix to the report on seals. In Turner's report on the scientific results of the voyage of the H. M. S. *Challenger* during the years 1873–76, etc. Zoology, vol. 1, pt. 4, pp. 139–234.

MIVART, ST. G.
1885. Notes on the Pinnipedia. Proc. Zool. Soc. London, pp. 484–501.

MÜLLER, O.
1898. Untersuchungen uber die Veranderungen welche die Respirationsorgane der Saugethiere durch die Anpassung an das Leben in Wasser erlitten haben. Jena. Zeitschr. f. Naturwis., vol. 25, pp. 95–230.

MURIE, J.
1870*a*. (Note on the anatomy of the walrus.) Proc. Zool. Soc. London, pp. 544–545.
1870*b*. Researches upon the anatomy of the Pinnipedia. Part 1. On the walrus (Trichechus rosmarus Linn.). Trans. Zool. Soc. London, vol. 7, pp. 411–464.
1870*c*. On Phoca groenlandica Mull. Its modes of progression and its anatomy. Proc. Zool. Soc. London, pp. 604–608.
1872. Researches upon the anatomy of the Pinnipedia. Part 2. Descriptive anatomy of the sea-lion (Otaria jubata). Trans. Zool. Soc. London, vol. 7, pp. 527–596.
1874. Researches upon the anatomy of the Pinnipedia. Part 3. Descriptive anatomy of the sea-lion (Otaria jubata). Trans. Zool. Soc. London, vol. 8, pp. 501–582.

OSBURN, R. C.
1903. Aquatic adaptations. No. 1, Adaptations to aquatic, arboreal, fossorial and cursorial habits in mammals. Amer. Nat., vol. 37, pp. 651–665.

OWEN, RICHARD.
1831. On the anatomy of the seal (Phoca vitulina). Proc. Comm. Zool. Soc. London, 1, pp. 151–154.
1866, 1868. On the anatomy of the vertebrates. Vols. 2 and 3. Longmans Green and Co., London.

Piersol, G. A.
1907. Human anatomy. Lippincott and Co., pp. 1–2088.
Reighard, J. and H. S. Jennings.
1901. Anatomy of the cat. Ed. 2, Henry Holt and Co., New York, pp. 1–498.
Rosenthal, F. C.
1831. Zur Anatomie der Seehunde. Nova Acta Acad. Caes. Leop.-Carol., vol. 15, pp. 313–348.
Thomson, R. B.
1909. Osteology of the Antarctic seals. Scottish Nat. Antarc. Exped., 8, Trans. Royal Soc. Edinb., vol. 47, pp. 187–201.
Todd, T. W.
1922. Numerical significance in the thoracicolumbar vertebrae of the Mammalia. Anat. Record, vol. 24, pp. 261–286.
Toldt, C.
1903–4. An atlas of human anatomy. Pts. 1–6. New York.
Weber, Max
1904. Die Saugetiere. Jena, pp. 1–866.
Williston, S. W.
1902. On certain homoplastic characters in aquatic, air-breathing vertebrates. Kansas Univ. Sci. Bull., vol. 1, pp. 259–266.
Wortman, J. L.
1894. Osteology of Patriofelis, a Middle Eocene creodont. Bull. Amer. Mus. Nat. Hist., vol. 6, pp. 129–164.
1921. On some hitherto unrecognized reptilian characters in the skull of the Insectivora and other mammals. Proc. U. S. Nat. Mus., vol. 57, pp. 1–52.

EXPLANATION OF PLATE

Plate 1

Mounted skeletons of an eared seal (Otariidae, genus *Callorhinus* below) and an earless seal (Phocidae, genus *Phoca* above) exhibited to show normal terrestrial positions.

○